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Climax Conditions and the Ecological Status of Pinus Strobus, Taxus Canadensis and Tsuga Canadensis in the Pine Hills Region of Indiana

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Some Comparisons Between Virgin Forest and Adjacent Areas of Secondary Succession

J. E. POTZGER *and* RAY C. FRIESNER

Additions to the Algal Flora of Indiana

CHARLENE COFFING

Algæ of Steuben County, Indiana. I

C. MERVIN PALMER

These papers are contributions No. 49, 50, 51 and 52, respectively, from the botany laboratories of Butler University. Address all communications regarding them to Butler University Botanical Studies, Butler University, Indianapolis, Indiana, U. S. A.

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CLIMAX CONDITIONS AND ECOLOGICAL STATUS OF PINUS STROBUS, TAXUS CANADENSIS AND TSUGA CANADENSIS IN THE PINE HILLS REGION OF INDIANA

By Ray C. Friesner and J. E. Potzger

Along Sugar creek in Montgomery and Parke counties in west central Indiana, where the stream cuts through the Mansfield and deep into the Borden sandstones, there are a number of areas characterized by deep canyons with almost perpendicular rock walls. Three of these areas are locally known as Turkey Run State Park, The Shades, and Pine Hills. The latter two are about two miles from each other, and these in turn are approximately eighteen and twenty miles respectively upstream from Turkey Run. The canyon walls of Turkey Run are largely Mansfield sandstone, while those of Pine Hills are Borden sandstone, the Mansfield having been eroded away.

Physiographically, the Pine Hills area is characterized primarily by the presence of four pronounced and narrow "backbones" which project for several hundred feet from the main plateau into which the canyons have been cut, thus causing the two streams which have done the cutting to follow very tortuous and meandering courses. Figure 1 presents a diagram map showing the relation of the "backbones" to each other and to the surrounding plateau.

Botanically this region exhibits a larger number of excellent and clear-cut forest ecological areas and associations than any other region in Indiana known to the writers. For example: there are wooded old flood-plain terraces along the meandering streams, where they have cut wider valleys (areas 1, 12 and 15, Figure 1); second terraces or still older flood plains now occupied by dense stands of deciduous forest trees (areas 2 and 13); upland plateaus into which the canyons have been cut (areas 6 and 14); Pinus-Tsuga slopes (areas 3, 7 and 10); transition areas between the preceding two (area 5); Tsuga-covered canyon walls (area 11); Pinus-Tsuga groves (area 8), and Taxus associations on north-facing canyon walls where the angle approximates 45 degrees (area 9). Figure 1 shows the relation of these areas to each other.

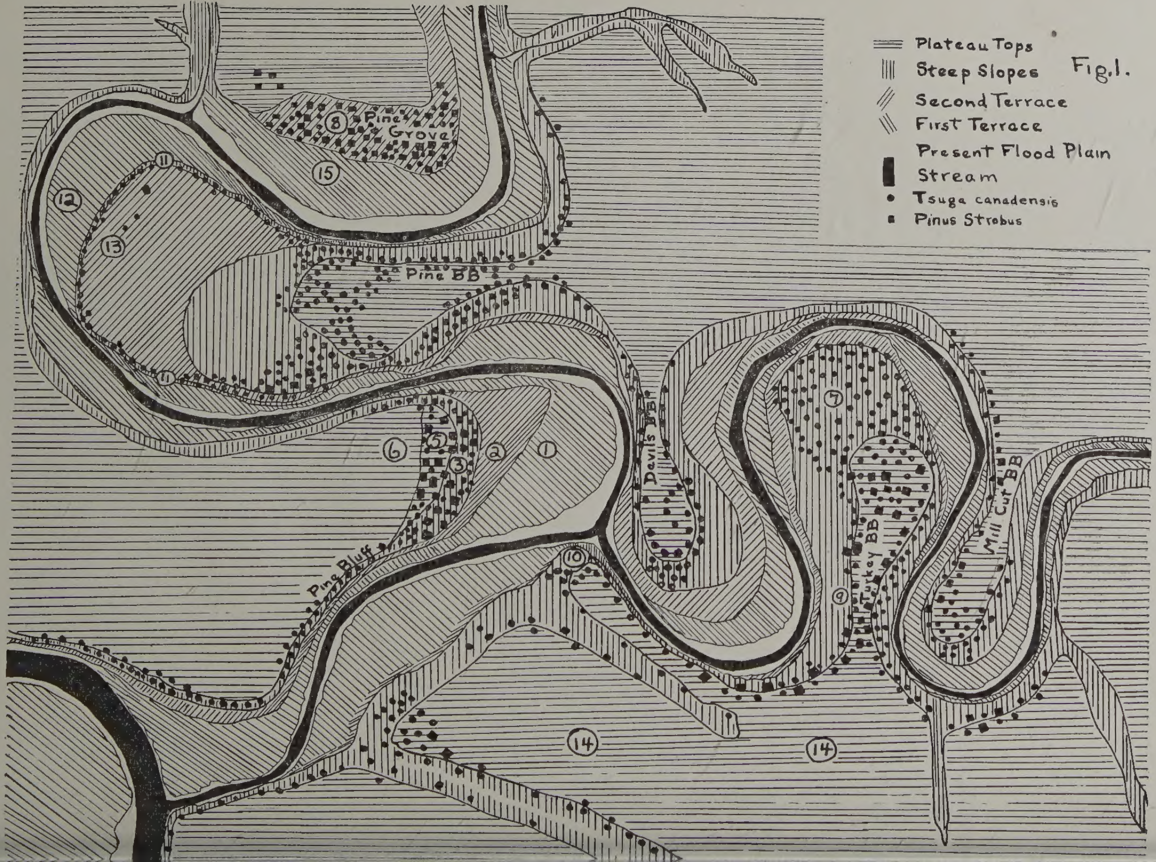
Plateau Tops
Steep Slopes
Second Terrace
First Terrace
Present Flood Plain
Stream
Tsuga canadensis
Pinus Strobus
Pine Grove
Pine BB
Pine Bluff
Devils BB
Turkey BB
Mill Cut BB
1
2
3
5
6
7
8
9
10
11
12
13
14
15

Fig. 1.

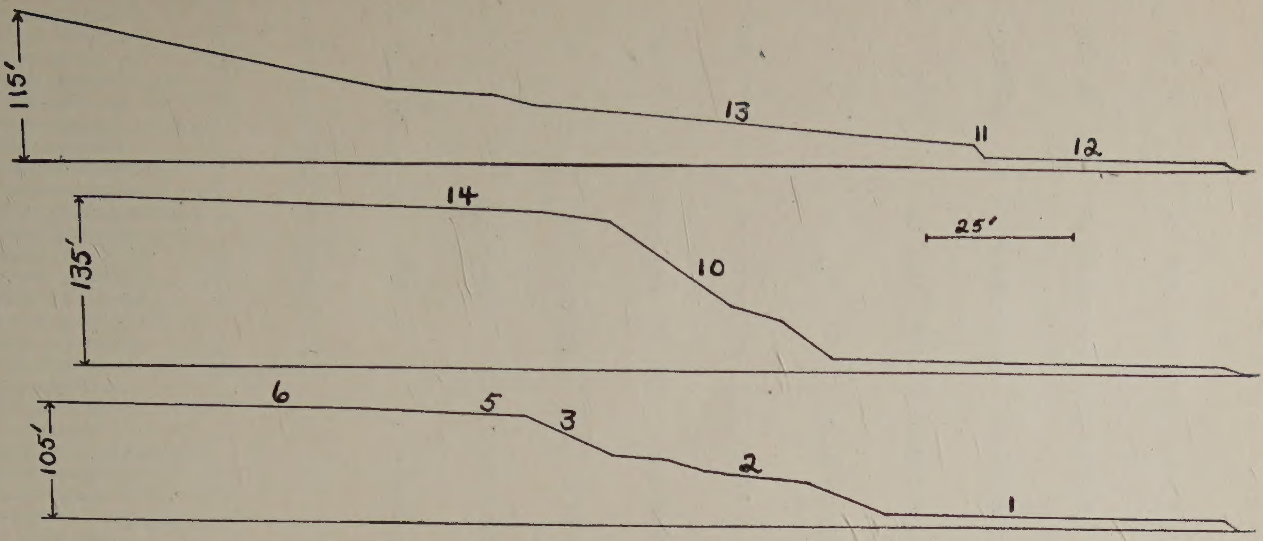

Fig 2. Profiles Showing Elevation of Areas

TABLE I

SUMMARIZED FREQUENCY GROUPS OF SPECIES IN EACH AREA STUDIED

	FREQUENCY GROUP[1] OF SPECIES IN DIFFERENT ASSOCIATIONS												
SPECIES	15[2]	12	1	2	13	6	14	5	3	11	7	8	9
Acer saccharum[3]	D	E	E	E	E	E	E	D	C	D	A	D	C
Dirca palustris	C	E	E	B	A	A				A		A	
Carpinus caroliniana	D	C	E	E	A	B	B		A	A	A	A	A
Vitis sp?	E	D	C	A	A	C	D			A	A	A	A
Fagus grandifolia			D	E	D	D	B	B	C	D	C	C	A
Viburnum acerifolium				E	D	C	C	E	D	D	A	D	B
Cornus florida	A		B	E	C	B	B	E	C	B	A	B	A
Ostrya virginiana	A	B	A	B	E	D	C	C	A	B	A	B	A
Sassafras variifolium			A	C		D	E	B	B	A	A	A	
Pinus strobus	A			A	A	A	A	E	E	A	A	E	
Tsuga canadensis	A			A	B		A	B	E	E	E	E	B
Taxus canadensis											A		E
Cercis canadensis	D	D	A							A			
Cornus alternifolia	D	D	A		A		A			A	A	A	A
Rhus toxicodendron	C	D	C		C		A			B	A	B	A
Cornus asperifolia	C	D			A		A			A			
Fraxinus lanceolata	C	D	C	A	C	A	A		A	B	A	B	A
Quercus alba	A	A	A	A	C	B	D	C	C	A	B	B	
Quercus velutina						A	D			A			
Quercus borealis maxima	A	A	B	C	B	B	A	D	C	B	A	B	A
Celastrus scandens	C		B							A			A
Platanus occidentalis	C	C	C										
Ulmus racemosa	C	C	C										
Asimina triloba		C	C		A								
Benzoin æstivale	A	C	A							A			
Juglans cinerea	B	C				A				A	A	A	
Acer negundo	B	B	C							A			
Carya cordiformis	A	B	C		A	A	A			A	A	A	A
Tilia americana	B	A	C	A			A			A	A	A	A
Juglans nigra	A	A	C						A				
Prunus serotina				C	B	A				A	A	B	
Acer rubrum				B	C	B	C	C	B	C	A	B	
Ribes cynosbati	A		A	B	A	C				B	A	A	
Carya ovata	A	A			A	A	C				A	A	A

Liriodendron tulipifera ..	A	B	B	A	A	B	A	A		A			
Fraxinus quadrangulata ..	A	A	B							A			
Æsculus glabra	A	A	B	A		A				A			
Gymnocladus dioica			B										
Hamamelis virginiana	A	A	A	A	B	A	A	B	A	A		A	A
Physocarpus opulifolius ..	A												
Maclura pomifera	A												
Morus rubra	A	A	A		A		A				A	A	
Rubus occidentale	A									A	A		A
Rubus allegheniensis	A						A		A	A	A	A	
Gleditsia triacanthos	A		A										
Evonymus atropurpureus	A	A											
Ptelea trifoliata		A											
Fraxinus americana		A									A		
Evonymus obovatus		A				A				A	A		
Celtis occidentalis		A											
Hydrangea arborescens ..		A			A					A	A		
Prunus americana			A										
Psedera quinquefolia			A	A		A		A					
Vaccinium vacillans				A									
Juniperus virginiana					A	A		A	A				
Ulmus americana					A					A			
Sambucus canadensis						A							
Nyssa sylvatica						A	A	A	A			A	
Cratægus sp?									A				
Populus grandidentata									A				
Amelanchier canadensis....									A	A	A		
Species in Group A..........	22	16	13	12	16	17	14	5	11	29	27	14	15
Species in Group B..........	5	5	8	4	4	6	3	4	2	6	1	8	2
Species in Group C..........	7	6	10	3	5	3	4	3	4	1	1	1	1
Species in Group D..........	4	6	1	0	2	3	3	2	1	3	0	2	0
Species in Group E..........	1	2	3	5	2	1	2	3	2	1	1	2	1
Total No. of Species..	39	35	35	24	29	30	26	18	20	40	30	27	19

[1] Frequency groups are those of Raunkiaer: A = 1—20 per cent; B = 21—40 per cent; C = 41—60 per cent; D = 61—80 per cent; E = 81—100 per cent.

[2] Areas number 1, 12 and 15 are first terraces above the present active flood plain.

Number 2 and 13 are second terraces, *i.e.*, higher older flood plain.

Number 6 and 14 are upland plateaus, the oldest areas of the region.

Number 3 and 7 are steep slopes up to the plateau.

Number 11 is a younger steeper slope occurring between areas 12 and 13.

Number 5 is a plateau area between areas 3 and 6. Physiographically it is nearly the same as areas 6 and 14 but ecologically it is transitional between areas 3 and 6.

Number 8 is a Pinus-Tsuga grove in an area physiographically similar to areas 2 and 13.

Number 9 is a steep slope containing a Taxus socies. It is different from areas 3, 11 and 7, in that it has much shallower soil.

The location of these areas is shown in Figure 1.

[3] Nomenclature is that used in Gray's Manual, 7 ed.

METHODS

A quadrat study was made of each of the above-mentioned areas except area 10. In each area twenty-five quadrats were marked off and studied. These quadrats were 25 feet on a side in all areas except area 1 where they were 50 feet, and area 9 where, on account of the size of the area, they were reduced to 10 feet. In each quadrat the total number of individuals of each species together with sizes in DBH. were listed. From these lists the composition of each area was tabulated in terms of percentages of quadrats in which each species occurred one or more times. These tabulations are all summarized in Table I, where each species is listed and the frequency group to which it belonged in each area is given. The frequency designations used are those of Raunkiaer, in which frequencies of 1 to 20 per cent belong to group A, 21 to 40 per cent to group B, 41 to 60 per cent to group C, 61 to 80 per cent to group D, and 81 to 100 per cent to group E.

OBSERVATIONS

Steep Slopes

Areas 11, 7 and 3 (see Figure 1) are steep slopes. Area 11 is the steepest of the three with an angle of 40 to 45 degrees, and is at present undergoing considerable topographic change as a result of erosion. Area 3 is the most stable of the three, *i. e.*, at present undergoing least erosion. It not only presents a less steep (24 degree) slope, but also its floor is more protected by leaf litter and mosses. Figure 2 is a series of profiles indicating the elevation of the various areas above the stream level. Horizontal position of areas is shown in Figure 1.

Table I shows a complete list of the woody species observed in this study. The species are arranged in order of frequency, *i. e.*, all species which occur in frequency group E in one or more areas are grouped together; next come those species which occur in frequency group D in one or more areas, and so on until in the last group are found only those species which occur in frequency group A.

Table II presents total number of species, and percentages and number of species in frequency group A and E in each of the different areas. Different areas of the same type are brought together and arranged in order of physiographic age.

TABLE II

Percentages and Numbers of Species in Frequency Groups A and E in the Different Areas. Different Areas of the Same Type Are Brought Together and Arranged in Order of Increasing Physiographic Age.

Area Number	Total No. Species All Gps.	Frequency Group A		Frequency Group E	
		Per Cent	Number Species	Per Cent	Number Species
11	40	73	29	2.5	1
7	30	90	27	3	1
3	20	55	11	10	2
15	39	56	22	2.5	1
12	35	46	16	6	2
1	35	37	13	9	3
13	29	55	16	7	2
2	24	50	12	28	5
6	30	56	17	3	1
14	26	52	14	8	2
9	19	79	15	5	1
8	27	52	14	6	2
5	18	28	5	17	3

Reference to Table I will show that area 11, which, because of amount of present topographic change, may be considered the youngest area physiographically, contains the largest number of species found in any area studied. Tsuga is the only class E species, and 73 per cent (Tables I and II) of the species present are in class A. Over 50 per cent of the remainder belong to group B, and over 40 per cent of the species which in one or more areas studied fall in group E, are found in group A in this area. This area thus presents ecologic evidence of physiographic instability.

Area 3, which undoubtedly is at present more stable physiographically than either area 11 or 7, contains but twenty species, and only 55 per cent of them belong to the lowest frequency group (group A), while 10 per cent belong to the highest frequency group. Pinus joins Tsuga as a class E species in this area.

Area 7 is intermediate between the former two in regard to physiographic age. It is also intermediate in total number of species present, number of species of low frequency (group A), and percentage of species of high frequency. The area is dominated by a dense stand of Tsuga with Pinus around the border, especially the upper border just before the Tsuga association gives way to the Acer-Quercus association of the top. It will be noted that these steep slopes are dominated by Tsuga or by Tsuga-Pinus associations.

Area 9 is a very steep (40-45 degree) slope on the north-facing wall of "Turkey Backbone." It is striking in that *Taxus canadensis* is the outstanding species of the area and is so dense that little else can become established. From Table I it will be noted that there are but nineteen species in the area and 79 per cent of these belong to group A. Thus an area of severe physiographic stress may be characterized ecologically by both small total number of species and high percentage of low frequency species.

FIRST TERRACES

Areas 15, 12 and 1 (Figures 1 and 2) are old flood-plain terraces, the latter two of which are probably never actually flooded any more by the stream. Area 15 may be inundated during the time of highest water level of the stream. These areas are not subject to the physiographic stress present in areas 11, 7 and 3, but they are physiographically young in the sense that they are not long removed from the period of stream action and have not had time to reach a more stable biologic condition which ultimately results from competition and ecological adjustment. Area 15 is physiographically the youngest and area 1 the oldest of the three, judging from the present height above the level of the stream. In area 15, Vitis is the only group E species, while *Acer saccharum* and *Dirca palustris* are group E species in both areas 12 and 1, and *Carpinus caroliniana* is also a group E species in area 1. These latter three species are found in groups D, C and E respectively in area 15.

Study of Table II, where the different areas are arranged in the order of increasing physiographic age, will show that as the age of any group of topographically similar areas increases, there is a corresponding decrease in total number of species present and in percentage and number of species occurring in group A (low frequency), while there is an increase in percentage and number of species occurring in group E (high frequency). Area 15 has 56 per cent of its species in the lowest frequency group (group A) and 2.5 per cent in the highest frequency group (group E); area 12 has 46 per cent in the low frequency group and 6 per cent in the high group; and area 1 has 37 per cent in the low group and 9 per cent in the high group. The biologic conditions thus point out area 15 as botanically the youngest and area 1 as the oldest of these three topographically similar areas, and this conclusion is in accord with physiographic observations.

Areas 11, 7 and 3 (Table II) show similar relations when compared with each other, except that Tsuga has dominated area 7 to such an extent that twenty-seven out of the total of thirty species occurring in that area are so scattered as to fall in the lowest frequency group, thus giving the lowest frequency species in this area a higher percentage than is shown by the same group in area 11, even though area 7 is physiographically older than 11.

SECOND TERRACES

Areas 13 and 2 (Figures 1 and 2) are second terraces from 15 to 20 feet above areas 12 and 1 respectively. Area 2 is without doubt older physiographically than area 13. The same set of relations (see Table II) hold here as in the above two sets of areas, *viz.*, increased physiographic age is accompanied by decreased total number species, and percentage and number of species in group A; and increased percentage and number of species in group E. Reference to Table I shows that while *Acer saccharum* and *Ostrya virginiana* are group E species in area 13, *Acer saccharum, Carpinus caroliniana, Fagus grandifolia, Viburnum acerifolium* and *Cornus florida* are group E species in area 2. In Table II it will be noted that second terrace areas (13 and 2) have considerably smaller number of species than physiographically younger first terraces (areas 1, 12 and 15).

Area 8 (Figure 1) is a Tsuga-Pinus grove physiographically comparable to areas 2 and 13. Here Pinus and Tsuga are each growing in 95 per cent of the quadrats studied and in an area where deciduous forest would certainly be expected when this area is compared physiographically with other areas of the region. It is difficult to explain on the basis of present information why these conifers are to be found in this area. It may be that soil moisture conditions here are quite different from other physiographically similar areas and more like the slopes where Tsuga and Pinus are found in other areas. Study of the physical conditions present in each of the areas considered in this paper is under way and will probably throw considerable light upon the edaphic conditions of each association.

PLATEAU TOPS

Areas 6 and 14 are plateau tops (Figures 1 and 2) and are the oldest physiographic areas of the region. Area 6 is somewhat lower in altitude than area 14 (Figure 2) and is probably younger physiographically. Table II shows the same relation between physiographic age and number and percentage of species in groups A and E for these areas as was shown above. *Acer saccharum* is the only group E species in area 6, while *Sassafras variifolium* joins it in group E in area 14. Fagus occurs in group D in area 6, but falls to group B in area 14. The reverse order is shown by *Quercus alba* in these two areas, *i. e., Q. alba* is a group D species in area 14, but falls to group B in area 6. *Quercus velutina* is also a group D species in area 14.

TRANSITION ZONE

Area 5 is transitional between areas 3 and 6 (Figures 1 and 2) both as to physiographic age and as to ecologic relations. The Pinus-Tsuga association of the steep slope (area 3) grades over, as the top of the slope flattens out, into the deciduous forest, *i. e.,* Acer-Fagus association. Reference to Table I shows that whereas Pinus and Tsuga were the dominant species of area 3 (steep slope), Tsuga drops to group B, while Pinus remains and *Viburnum acerifolium* and *Cornus florida* join it in group E, and *Acer saccharum,* which is dominant in area 6 (plateau top) falls into group D in this transition zone. As we go up the slopes, Tsuga first appears on the lower parts, and farther up Pinus comes in with it and continues to the top. Pinus also extends into the transition zone and finally gives way to the broad-leaved Acer or Acer-Fagus climax. That is, as we advance from the terraces to the older plateaus, we pass from broad-leaved Acer-Fagus, etc. (area 2), through Tsuga, Tsuga-Pinus (area 3), Pinus-Cornus-Viburnum (area 5) to Acer-Fagus (area 6).

Area 7 shows a similar relation between Tsuga and Pinus. The area is so decidedly a Tsuga association that 90 per cent of the thirty species present fall in group A. Pinus occurs only as an upper transitional fringe between the Tsuga of the steeper slope and the deciduous Acer-Quercus-Sassafras association of the plateau (area 14).

Areas 11, 7 and 3 form a group of topographically similar areas; similarly areas 15, 12 and 1; areas 13 and 2; and areas 6 and 14. These groups of areas are physiographically older as groups in the order named. Reference to Table II will show that the relations regarding percentage of species occurring in the various frequency groups which pertain among areas of the same group do not hold well when comparing one group of areas with another group of areas of different topographic age. Cowles (3) has shown that topographic cycles may require so much greater duration of time than vegetative cycles that any particular topographic area may go through many complete vegetational cycles before it has had time to advance from topographic youth to topographic old age. These first terraces (areas 15, 12 and 1) are undoubtedly more recent physiographically than the second terraces (areas 13 and 2) and the pre-erosion plateaus (areas number 6 and 14). They show no relation to each other as groups except that the younger areas (1, 12 and 15) show a larger total number of species than the older areas (2 and 13, 6 and 14, respectively).

CLIMAX CONDITIONS

It can hardly be doubted that *Acer saccharum* is a climatic climax species of this region. Reference to Table I shows that it occurs in frequency group E in a larger number of areas studied than any other species and is in group E in all except the physiographically youngest areas. It occurs in 50 per cent or more of the quadrats of all areas studied except area 7, which is so predominantly a Tsuga association that 90 per cent of all species in the area belong to group A. It is significant that *Quercus alba* and *Fagus grandifolia* are the only species, besides Tsuga, occurring outside of group A in this area (area 7). It is further significant in this connection that wherever *Acer saccharum* falls below 81 per cent, except in area 15, the species belonging to class E are either Pinus, Tsuga or Taxus, and in all cases where it is outside of group E the area is physiographically young. Since it is the dominant species in all areas which are physiographically older, it must be considered a climatic climax of the region.

Three species occur in every area studied. They are: *Acer saccharum, Ostrya virginiana* and *Quercus borealis maxima*. Four other species occur in all areas except one. They are: *Carpinus caroliniana, Cornus florida, Fraxinus lanceolata* and *Quercus alba*. Reference to Table I will show that none of these species except *Acer saccharum* occurs in group E in more than two areas, and where they do fall into group E the area is in every case physiographically young. In the older areas these species all (except *Acer saccharum*) occur in frequency groups below the 81 per cent minimum of group E. In no area do they even approach the high frequency of *Acer saccharum*. This apparently indicates that these species are tolerant of a wider range of habitat conditions than other species and not that they are climax species.

The condition of *Fagus grandifolia* is also worthy of mention. Through Ohio, southern Michigan and most of Indiana, this species is often codominant with *Acer saccharum.* Farther west in Indiana and Illinois, Fagus drops out and Acer is left to make up the climax. Reference to Table I will show that Fagus occurs in class E in but one area, *viz.,* area 2. In areas 6 and 14, where we should expect it to fall in group E if it is a climax species, we find it falling into groups D and B respectively. It would seem, therefore, that this region must be on the border between the Acer-Fagus climax on the one hand and the more western Acer climax on the other. It should be noted that *Quercus alba* and *Q. velutina* each fall into group D in these plateau areas where Fagus is less abundant. This might indicate some relation to Quercus-Carya association, but Carya never occurs above group C in frequency. In actual numbers, Acer far surpasses either of the Quercus species, so that it would seem that the oldest regions are truly Acer-climax rather than Acer-Quercus-climax areas. Similar conditions with respect to the frequency of *Acer saccharum* and *Fagus grandifolia* were found in our Blue Bluffs study (Cain, Friesner, Potzger (1)) where Fagus falls into class E in but one of the six areas in which Acer shows a 100 per cent frequency.

In Table III are listed those species which show complete fidelity in the different types of areas of this region. It will be noted that ten species show complete fidelity to the first terrace areas and one additional species occurs in both first and second terrace areas to the exclusion of all others. With the exception of *Maclura pomifera,* these species showing complete fidelity to the terrace areas are species which one would expect to find in mesophytic areas young with respect to nearness to climax condition.

Four species: *Taxus canadensis, Amelanchier canadensis, Populus grandidentata* and *Cratægus* sp. show complete fidelity to the slope areas in so far as this region is concerned. The latter three are species regularly found on river bluffs in the more xerophytic stages of bluff succession toward the mesophytic forest.

The table shows but one species with complete fidelity to the upland plateau. This species, *Sambucus canadensis,* evidently is one which merely happened to be present since it occurred in but three quadrats of the entire upland areas. The table thus shows a reduction in num-

TABLE III

ILLUSTRATING THE DEGREE OF FIDELITY SHOWN BY DIFFERENT SPECIES IN THE DIFFERENT ASSOCIATIONS OF THE PINE HILLS REGION

	Limited to 1st Terraces Areas 1, 12, 15	Limited to 1st and 2nd Terraces Areas 1, 12, 15, 2, 8, 13	Limited to Slopes Areas 3, 7, 9, 11	Limited to Plateau tops Areas 5, 6, 14	Occurring in all types of areas
Platanus occidentalis	x				
Ulmus racemosa	x				
Gymnocladus dioica	x				
Physocarpus opulifolius	x				
Maclura pomifera	x				
Gleditsia triacanthos	x				
Evonymus atropurpureus	x				
Celtis occidentalis	x				
Prunus americana	x				
Ptelea trifoliata	x				
Asimina triloba		x			
Taxus canadensis			x		
Amelanchier canadensis			x		
Populus grandidentata			x		
Cratægus sp.			x		
Sambucus canadensis				x	
Acer saccharum					x
Carpinus caroliniana					x
Vitis sp?					x
Fagus grandifolia					x
Cornus florida					x
Ostrya virginiana					x
Sassafras variifolium					x
Pinus strobus					x
Tsuga canadensis					x
Cornus alternifolia					x
Rhus toxicodendron					x
Fraxinus lanceolata					x
Quercus alba					x
Quercus borealis maxima	x				
Carya cordiformis					x
Carya ovata					x
Tilia americana					x
Ribes cynosbati					x
Smilax sp?					x
Ulmus fulva					x
Liriodendron tulipifera					x
Æsculus glabra					x
Hamamelis virginiana					x
Morus rubra					x

ber of species showing high fidelity to a particular type of area as the areas become successionally and physiographically more mature.

Areas successionally and physiographically younger have a large number of species which get a foothold on the new area. As the area progresses toward maturity, those species which are better adapted to the climatic and physiographic conditions crowd out the many species which made their appearance when the area was younger. This indicates that the larger number of species showing complete fidelity to the younger areas (*i. e.,* first terraces as compared with plateau tops) is not due so much to the limited range of adaptation to the physical conditions of the habitat on the part of the species showing this fidelity as it is the biotic factor of competition. That is, those species which are limited to the first terraces may be absent from the other regions not only because of inability to adapt themselves to the inanimate aspects of the other habitats, but also because of greater competition and therefore inability to adapt themselves to the biotic aspects of the environment of the other areas. In either case, greater degree of fidelity exhibited by a species means more limited range of adaptation to habitat conditions, either physical or biotic, or both.

Table III also shows twenty-four species with complete lack of fidelity. These species are those found typically in the mixed mesophytic forests of Indiana. The presence in this group of such species as *Carya* spp. and *Sassafras variifolium* indicates that perfect climax conditions have not yet been attained, since these forms are characteristic of more xerophytic habitats.

It is of interest to compare this list of twenty-four species showing complete lack of fidelity with the list of species found in all altitude zones above the flood plain in the Blue Bluffs region (1). There are eighteen species common to the nonfidelity groups of both regions. There are three species, *viz., Pinus strobus, Tsuga canadensis* and *Cornus alternifolia,* which occur in the Pine Hills, but not in the Blue Bluffs region, while there are three others, *viz., Ribes cynosbati, Smilax* sp. and *Hamamelis virginiana,* which appear in all areas of the pine Hills region, but are limited more narrowly in the Blue Bluffs region.

ECOLOGICAL STATUS OF TAXUS, TSUGA AND PINUS

Taxus canadensis is found in but three counties in Indiana. These are all adjoining counties in the west central portion of the State, *viz.,* Parke, Montgomery and Putnam (5, 6, 7, 13). Locally its occurrence is always on steep slopes or canyon walls where the soil layer is insufficient to support species with deeper root systems and where there is sufficient protection from wind and sun to insure moister conditions. Probably the nearest station for this species outside of the above-mentioned counties is the Sugar Grove region of Ohio, which is over 175 miles east and somewhat south of these Indiana stations. The species quite obviously has a strikingly disjunct distribution in this southern portion of its range, and, since it is distinctly a northeastern species, it is here considered to be a glacial relict. As the species followed the glacier in its northern retreat, it has been crowded out by other species better adapted to environmental conditions except in these few places where the moister canyon walls make a sufficiently favorable habitat and the soil depth is insufficient to support its chief competitors.

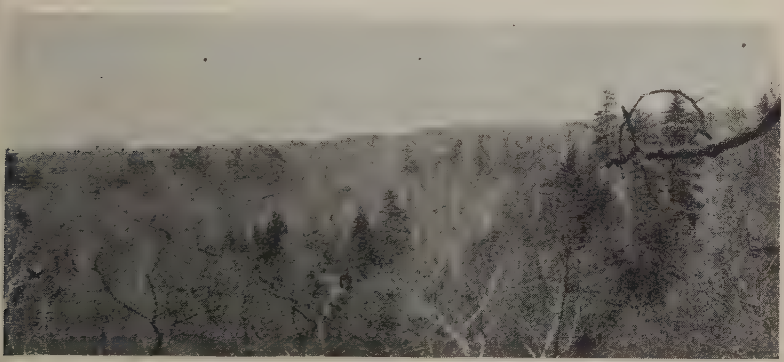

FIGURE 3. *Tsuga is limited to steep slopes and bluffs (except in area 8) and often follows courses of the streams.*

The ecological significance of *Tsuga canadensis* is not so evident as is the case with Taxus. In previous papers (8, 9) we have shown that Tsuga is limited in its distribution in Indiana to steeper slopes and canyon walls and that analyses of the physical factors of its environment show that it is in a somewhat more rigorous habitat than is occupied by the climax species of the region. The greater rigor of its habitat is exhibited in higher evaporation rate, lower soil moisture and greater soil temperature fluctuations where the soil of its habitat is deeper; and in insufficient soil depth to support its usual competitors where it occurs on the steeper slopes and rocky canyon walls. These physical data, together with the disjunct distribution, led us to the conclusion that *Tsuga canadensis* is a relict species. In our former papers we left unsolved the problem as to what type of relict condition is illustrated. This problem, involving a consideration of the general distribution of the species in its entire North American range, is a matter which is at present under study for a future paper. The area here studied not only supports our former conclusion regarding the relict nature of Tsuga, but it also yields data bearing upon the contention that Tsuga is a codominant with the Beech-Maple climax. As shown by Daubenmire (5), Tsuga occupies plateau tops in physiographically older areas along with Acer and Fagus at Turkey Run. But his analysis of physical factors shows clearly that there is always a lower soil moisture content and a slightly higher evaporation rate in Tsuga associations, thus indicating that it is occupying a somewhat more xerophytic habitat than Acer and Fagus, even though the physiographic conditions may seem similar. In the Pine Hills region, Tsuga characteristically occupies such physiographically young areas as steep slopes, but is also found in 100 per cent of the quadrats in area 8, which is a second terrace physiographically similar to areas 2 and 13, in neither of which is it found. Analysis of physical factors is under way and will probably show that this second terrace area (area 8) possesses a more xerophytic soil condition than other second terrace areas of this region.

The ability of Tsuga to dominate a particular area is very well shown in area 7, where it is the only group E species, and 90 per cent of all species fall in group A. (See Tables I and II.)

The occurrence of Pinus along with Tsuga shows that these areas are not entirely mature, since Pinus is generally considered to be a preclimax species (Cowles, 2). This leaves *Acer saccharum* as the present climax species of the region and Tsuga as relict colonies of a former wider distribution and possibly a former climatic climax. As this former climate has changed, Tsuga has been crowded out except in those areas which, because of their particular physiography, come more nearly presenting the former climatic conditions. In this connection it is of importance to note that the distribution of Tsuga in Indiana (Montgomery, Parke, Putnam, Morgan, Owen, Brown, Jackson, Lawrence, Jennings, Clark, Floyd and Crawford counties (6, 7)) is parallel with the geologic outcrops which permit the formation of canyons or steep slopes, and it is more prolific in growth in those areas where the habitats are not so far from the degree of mesophytism demanded by Acer or Acer-Fagus associations. The distribution of Tsuga in southeastern Ohio is closely parallel with regard to local habitats to that in Indiana.

Pinus strobus presents a still more difficult problem in regard to the ecological significance of its distribution in Indiana. It occurs as a native species in seven counties (Lake, Porter, Laporte, St. Joseph, Warren, Fountain and Montgomery (4, 6, 10, 11)). These stations fall into two groups, *viz.*, a Lakes group comprising the areas of the first four counties, and a West Central group comprising the next three counties. This distribution is again sufficiently disjunct to consider *Pinus strobus* a relict species, but our present study throws no light upon the problem as to what type of relict it may be.

In the Pine Hills region, *Pinus strobus* is on the fringe of the hemlock stands when the latter are on slopes. In area 3, which is a slope area, it shows a frequency of 88 per cent associated with Tsuga, which shows 100 per cent frequency. Its main distribution is in the upper part of the slope, and as the slope merges into the upland plateau (area 5), Pinus shows an 88 per cent frequency in a transition zone where *Acer saccharum* shows 80 per cent; *Cornus florida*, 92 per cent; *Viburnum acerifolium*, 88 per cent; and *Tsuga canadensis* falls to 36 per cent. In area 7, which is another dense Tsuga slope (with Tsuga showing 100 per cent frequency), Pinus occurs on the fringe only as the Tsuga slope merges into the upland plateau.

These facts seem to indicate that Pinus occupies a position in areas slightly more xerophytic than those where Tsuga and Acer are dominant. Its presence in greater abundance in the transition zone may be due to the fact that it can compete better with Acer, Cornus, Quercus and other deciduous species than Tsuga can. And all of this in turn may mean that in this region Pinus may have occupied in the past a climax position prior to Tsuga and Acer. That is to say, Pinus may once have been the climatic climax of this region in postglacial time; but, as the climate and other environmental conditions changed, Tsuga may have become the climatic climax, only to be supplanted in turn with further change by Acer as the climatic climax. Both of the supplanted climaxes persist today only as relicts in isolated areas where the particular habitat sufficiently approaches the former condition to enable them to compete successfully with Acer. In this connection it is significant that in area 5, where Pinus reaches 88 per cent and Tsuga only 36 per cent frequency, and in area 8, where Pinus reaches 95 per cent and Tsuga 100 per cent frequency, *Acer saccharum* occurs in 88 per cent of the quadrats. From gross physiographic observation alone, the usually accepted notion that Pinus is more xerophytic and Tsuga more mesophytic is substantiated, except in area 8, where it is coexistent with Tsuga. It remains to be determined, as a part of our next season's work, whether physical studies will reveal the areas occupied by Pinus to be more or less xerophytic than those occupied by Tsuga.

SUMMARY

1. *Tsuga canadensis* is a group E (Raunkiaer's frequency grouping) species in all steep-slope and canyon-wall areas of the Pine Hills region of Indiana.
2. This species is limited to the above slopes except on one second-terrace area, where it occurs along with *Pinus strobus,* both of which are group E species on this terrace area.
3. *Pinus strobus* characteristically occurs as an upper-fringe species in the belt transitional between Tsuga and deciduous hardwoods of the upland plateaus.
4. *Taxus canadensis* occurs in several small areas, all of them on steep north-facing slopes where the growth of the species is so dense as to reduce almost all accompanying species to Class A frequency.
5. *Taxus canadensis* is considered to be a glacial relict species.
6. *Pinus strobus* and *Tsuga canadensis* are also considered to be relict species of a former climatic climax, both having at one time been climatic dominants, but as the climate has changed in postglacial time, they have given way to Acer and Fagus as present climatic dominants.
7. *Acer saccharum* is the dominant species of the region.
8. *Fagus grandifolia,* which occurs as a climax species in many parts of Indiana, does not show dominance here.
9. As the age of topographically similar areas increases, there is a decrease in percentage of species of low frequency and an increase in percentage of species of high frequency.
10. In so far as this region is concerned, areas physiographically younger show larger numbers of species with complete fidelity to the particular type of area than areas more mature.

LITERATURE CITED

1. Cain, S. A., R. C. Friesner and J. E. Potzger. A comparison of strip and quadrat analyses of the woody plants on a central Indiana river bluff. Butler Univ. Bot. Stud. 1:157-171. 1930.
2. Cowles, H. C. The physiographic ecology of Chicago and vicinity; a study of the origin, development and classification of plant societies. Bot. Gaz. 31:145-182. 1901.
3. —— The causes of vegetative cycles. Bot. Gaz. 51:161-183. 1911.
4. Coulter, S. Notes on distribution of forest trees in Indiana. Indiana Acad. Sci. Proc. 1914:167. 1915.
5. Daubenmire, Rexford. Relation of certain ecological factors to the inhibition of forest floor herbs under hemlock. Butler Univ. Bot. Stud. 1:61-76. 1930.
6. Deam, C. C. Trees of Indiana. 2 ed. Indiana Dept. Conservation Pub. 13. 1921.
7. Erlanson, Eileen W. A list of plants chiefly from Putnam county, collected 1910-15 by Earl J. Grimes. Indiana Acad. Sci. Proc. 1923:123-163. 1924.
8. Friesner, R. C., and J. E. Potzger. Studies in forest ecology. I. Some factors concerned in hemlock reproduction in Indiana. Butler Univ. Bot. Stud. 2:133-144. 1931.
9. —— Studies in forest ecology. II. The ecological significance of hemlock in Indiana. Butler Univ. Bot. Stud. 2:145-149. 1931.
10. Peattie, D. C. Flora of the Indiana dunes. Field Museum, Chicago. 1930.
11. Pepoon, H. S. Flora of the Chicago region. Chicago. 1927.
12. Price, Gladys, and Winona H. Welch. Enumeration of the vascular flora of a limestone area of the Bloomington quadrangle, Monroe county, Indiana. Indiana Acad. Sci. Proc. 39:127-131. 1929.
13. Wilson, Guy West. Notes on some new or little known members of the Indiana flora. Indiana Acad. Sci. Proc. 1905:165-167. 1906.

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SOME COMPARISONS BETWEEN VIRGIN FOREST AND ADJACENT AREAS OF SECONDARY SUCCESSION

By J. E. Potzger and Ray C. Friesner

The almost unbroken deciduous forest of Indiana of a century ago has been reduced to isolated patches, and few of the remaining timbered areas may truly be termed virgin forest. These small tracts of undisturbed forest are thus of great ecological importance. One such small area of undisturbed forest is owned by Mr. August Mauntel, six miles southwest of Holland in Dubois county. Mr. Mauntel is an old settler in Dubois county and has seen the region develop from forest primeval to a busy agricultural community. He says that the area in question has been disturbed very little by cultural influences. Minor changes, of course, have occurred as a result of some necessitated drainage in the neighborhood, but this influenced the upland where the area of study is located but very little. About fifteen years ago most of the timber still remaining on the farm was cut except the wooded area studied in the present paper. Much of the timber in the adjacent lowland had been Liriodendron and *Juglans nigra,* while the forest of the higher hills consisted chiefly of oak and hickory. The present wooded area is listed as classified forest with the Indiana Forestry Department. Fifteen acres on the north (Section A) have never been cut and have suffered but little from grazing (about fifteen years ago cattle could roam the forest from adjacent fields during the winter, but little damage was done); about twelve acres on the southwest (Section B) were partially lumbered fifty-five years ago, *i. e.,* the large trees were cut; the southwest corner (Section C) was entirely cleared seventy years ago and has since been permitted to develop into forest according to the natural law of succession of the region. This offered an excellent opportunity for comparative study of undisturbed forest and two stages of secondary succession. Dead and fallen trees have been and are removed annually.

METHODS OF STUDY

The primary aim was to study the woody species both as to climax and successional features, especially as to reproduction, number of species represented in the various areas and constancy of the climax. To this end fifty quadrats of 100 square meters each were laid out in each of the three types of wooded sections. The quadrats comprised about 10 per cent of the total area.

A strong cord was measured off in ten-meter lengths and loops tied; these were slipped over stakes driven into the ground at each corner of a quadrat; direction was held by aid of a pocket compass. One person laid out the quadrats, another called the species and made measurements of DBH. of all woody plants one inch or over in diameter, while a third person made the tabulations according to quadrats numbered in proper succession. Diameter measurements were made with a pair of tree calipers. Trees one inch or more in diameter were measured, all woody plants below one inch in diameter but a meter or more in height were counted and tabulated, and in a one-meter quadrat in each ten-meter area the seedlings of woody species were listed.

PLANTS OF THE GROUND COVER

The floor of the forest was remarkably devoid of both herbaceous and woody species. *Rhus toxicodendron* was, without doubt, the most frequent species. Some of the more common species were: *Botrychium virginianum, Polystichum acrostichoides, Phegopteris hexagonoptera, Agrostis perennans, Brachyelytrum erectum, Iris cristata, Hieracium scabrum, Heuchera americana, Desmodium rotundifolium, Gillenia stipulata* and occasionally *Liparis liliifolium.*

GENERAL ASPECT OF SECTION A—VIRGIN TIMBER

Physiographically the whole area is a low elevation of rather stony soil. The crowns of the trees in Section A form a dense canopy, giving a very subdued light on the floor of the forest. The outstanding features are the abundance of large trees widely spaced, the sparse herbaceous cover and the scattered representation of seedlings of the dominant species (Table I). In certain patches, *Rhus toxicodendron* was the most prominent member of the ground flora; in fact, at times it covered the ground completely. Humus and decaying leaves formed a deep cover layer on the soil. The three areas are all typical oak-hickory forest. Not only is the virgin timber area (Section A) of this type, but the developing Section C is, again, reverting to oak-hickory climax through various stages of succession from open field to forest. Of the early successional stages there still remain such relics as *Rhus copallina*, *Rubus* sp., *Tecoma radicans* and *Sassafras variifolium*, as well as dense stands of Liquidambar.

Section A naturally excells in the greater abundance of large trees, of which the oaks have by far the greatest number; *Quercus alba*, with its eighty-eight stems above 1 inch DBH., and *Quercus velutina*, with twenty-nine stems, taking the lead (Table I). Of course, the combined Carya group, with a total of 189 stems, outnumbers that of Quercus with 128 stems, but Quercus outclasses Carya by greater size of stem. Carya has a total of 900 diameter-inches, while Quercus has a total of 1356 diameter-inches in the fifty quadrats studied. This is an average of 4.8 inches for Carya and 10.5 inches for Quercus. In fact, the stems of Carya are conspicuous by their small size, most of them being below 12 inches. The wide spacing of the trees tells a graphic story of great mortality among the young trees which probably germinated in the shade, which may even have survived to reach a diameter of a few inches and, under the stress of increased demand on the products of photosynthesis and water, found the habitat lacking in adequate supply of light and moisture. This is in full accord with experimental evidence obtained by Stallard (5). Evidently the process of perpetuation of a climax forest is more a manner of establishing the dominant species in open places which occur when trees die or are blown down, than a continuous crowding in of young growth between the crowns of older trees. No doubt most of the younger trees tabulated in a survey will never reach maturity. To cite an example, Carya is represented by 174 stems below 1 inch DBH. and Quercus by 143, yet, only thirty-five stems of Quercus over 15 inches and only seventeen of Carya 10 inches or over are present. Mortality must certainly be high among Fraxinus species, with 475 stems below 1 inch and only two trees above 10 inches.

It seems quite evident that the present oak-hickory woods is typical, permitting the conclusion that the much-pictured forest of giant trees of the primeval forest was made up primarily of trees 30 to 36 inches DBH., and trees above that size were the exception rather than the rule. Random measurements of all large oaks seen in Section A disclosed them to be within the 28 to 32 inch DBH. range. This is also substantiated by Table III of Cain's (2) paper dealing with virgin forest in Spring Mill State Park. His figures in general are quite comparable with those of the present study. In twenty-five quadrats 10 by 10 meters he lists 309 stems of which but three are above 30 inches DBH.; in fifty quadrats of the present study there are 533 stems with five trees of 30 inches or over. The same features are quite evident in Dillon's woods, a piece of virgin timber in Dubois county, which was observed during a general survey.

Section A is also unique on account of the absence of the common second layer trees, *i. e., Carpinus caroliniana* and *Ostrya virginiana.* In this respect, too, the Mauntel woods parallels Donaldson's woods (Cain (2), Table III). The only second layer tree which was present in any worthwhile representation was *Cornus florida.* In the frequency classes (Table II) for the three sections it was persistently present in class E. In Section A it appeared in 88 per cent of the quadrats. *Diospyros virginiana* was present in 34 per cent of the quadrats, indicating that it is able to germinate successfully in shade and compete with the dominant species in the earlier stages, but finds these environmental conditions intolerable with increasing size and age. Seeding is apparently carried on by opossums from several trees along the border of woods and field.

Acer saccharum and *Fagus grandifolia* have a very negligible representation and it seems that they will not form the climax forest here, since they have not established themselves in the developing area C during the past seventy years.

SECTION B—PARTLY CUT-OVER

This section was outstanding by trees of smaller size-range and patches of dense undergrowth, otherwise resembling more the virgin timber area. In the case of *Quercus alba* the size difference is not so pronounced. Section A had twenty-seven trees of this species of 20 inches or over DBH., while Section B had twelve trees of that size. The cutting of trees admitted more light, the moisture of the soil increased by the elimination of some of the stand and this resulted in more rapid growth. The section also shows a marked Quercus-Carya aspect. *Cornus florida* is the only second-layer tree represented, having a frequency of 88 per cent, which is the same as in Section A (Table I). *Quercus alba* shows a more marked increase in number of trees in the size range of 1 to 10 inches DBH. In Section B there are ninety-two, while Section A has but fifty-five such young trees. This points again to the conclusion that reproduction in undisturbed timber is more a

DENSITY OF TREES 1 INCH DBH. OR OVER

A, Virgin timber; B, partly cut fifty-five years ago; C, entirely cleared seventy years ago and left to natural succession.

SPECIES		DBH. IN INCHES																																
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	
Acer saccharum	A	1	2	2																														5
	B			1																														1
	C			1																														1
Acer rubrum	A	3		1	1																													5
	B			1																														1
	C	2	7	2	2	4		2						1																				20
Betula nigra	A											1																						1
	B																																	—
	C																																	—
Carya alba	A	2	2	1	1	1	1		3		1	1				1																		14
	B	7		3	2	1					1	1																						15
	C			1																														1
C. glabra	A	4	7	10	6	10	9	8	5	2	3	2	1	1																				68
	B	11	18	23	10	6	5	1		1																								75
	C	6	5	2	3		2		1			1																						20
C. laciniosa	A																					1												1
	B																																	—
	C																																	—
C. ovata	A	20	19	14	13	4	11	7	7	4	2	2	1		1																			105
	B	5	4	10	1	2	1	3	1	1	1																							29
	C	5	5	5	1	2					1		1																					20
C. cordiformis	A		1																															1
	B																																	—
	C																																	—
Cornus florida	A	38	21	6	2																													67
	B	30	19	21	4	2																												76
	C	39	39	32	8	7	3																											128
Cercis canadensis	A	6	1	1																														8
	B	3	1																															4
	C																																	—
Diospyros virginiana	A	2																																2
	B	1																																1
	C	16	5	4	1	2	1				1																							30

Species		DBH, in Inches																															
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	
Fraxinus americana	A	16	5	5		1	1		1	1		1			1																			32
	B	3	7	1	2	4	1	1																										19
	C	1	2	3	2	1		1																										10
F. lanceolata	A	36	6	3	2		2			1																								50
	B	4	1	1		1				1																								8
	C	9	5	5																														19
F. pennsylvanica	A	1																																1
	B																																	—
	C	1	2																															3
Juniperus virginiana	A	1																																1
	B																																	—
	C	2	1	2																														5
Juglans nigra	A																																	—
	B		1																															1
	C																																	—
Liriodendron tulipifera	A																																	—
	B																																	—
	C						2	1	3	1									1															8
Liquidambar styraciflua	A	1																																1
	B																																	—
	C	22	16	26	18	7	6	6	4	2		3	1																					111
Morus rubra	A	1	1	1																														3
	B	3																																3
	C																																	—
Nyssa sylvatica	A	7	4	4														1																16
	B	1																																1
	C	1		1						1																								3
Platanus occidentalis	A											1								1														2
	B																																	—
	C														1																			1
Prunus americana	A																																	—
	B																																	—
	C	4																																4
P. serotina	A	12	5																															17
	B	7		1							1																							19
	C	1			1																													

Quercus alba	A	18	3	10	7	5	2	3	3	1	3	2	1				1	1		1	2	3	5	1	5	4	2		1		1	2	1	88
	B	10	10	25	11	14	7	3	5	6	1			1	1	1		1	1	2		2	1	3	3	1					2			111
	C	2	10	12	11	20	12	6	4	5	11	5	3	3	2								1											107
Q. imbricaria	A	1	1				1																											3
	B														1																			1
	C	2	1	3	2		1	1	2				1																					13
Q. borealis maxima	A	2							1		1			1	1			1		1														8
	B				1		1			1	1	2											2											8
	C	2	3						1			1		1						2														10
Q. velutina	A	3	3		1			1	2	1	2		1	6	3	2	1			2													1	29
	B		2	1	1		3	5	6	6	9	6	3	6	1	1		1																51
	C	23	12	4	5	1					1				1			1																48
Q. palustris	A																																	—
	B																																	—
	C	1	2	2	2	2	1		2	1		1		1							1													16
Q. stellata	A																																	—
	B	4	5	4	5	2	5	2	2	5		2			1	1							1											39
	C	17	5	7	3	4	5	4	4		1	1			1			1																53
Q. bicolor	A																																	—
	B																																	—
	C	1																																1
Q. marylandica	A																																	—
	B							1																										1
	C																																	—
Robinia pseudo-acacia	A																																	—
	B																																	—
	C	3	1	1																														5
Rhus copallina	A																																	—
	B																																	—
	C	4	3																															7
Sassafras variifolium	A	3	1	1																														5
	B	6																																6
	C	27	26	13	3																													69
Ulmus americana	A	4	4	1						1																								10
	B	2	2	1																														5
	C						2									1																		3
U. fulva	A			1																														1
	B	1		1																														2
	C		1	1																														2

case of occupying ground vacated by death of old trees, than continuous growth to maturity under the crowns of an established forest canopy. Evidently, trees occupy all the ground which the available water and light permit, and so limit reproduction in that area to replacement only. *Quercus velutina,* with thirty-three trees of 1 to 10 inches DBH., and *Quercus stellata,* with thirty-four such stems, also tell a story of increased reproduction as places were vacated by older trees. There is no evidence of extreme reversal to secondary succession in this partly cut-over area, since the common early successional species, such as *Rhus copallina,* Sassafras and Liquidambar, which are so prominent in Section C, are almost absent here. Fraxinus is also much reduced in number of stems (Table II).

SECTION C—ENTIRELY CLEARED SEVENTY YEARS AGO

The outstanding features of this area are the smaller diameter of trees, dense stands, with intermittent open tracts, the presence of species of earlier successional stages and the lack of deep humus layer so evident in the other two sections. Copses were frequent, and many open patches were covered with lichens and xerophytic mosses. The latter told a graphic story of the effects of erosion after the land had been cleared. This area had about 35 per cent more species in the flora than the other areas. Developmental stage was indicated by such frequencies in woody species as: *Diospyros virginiana,* 54 per cent; *Juniperus virginiana,* 44; *Sassafras variifolium,* 36; *Liquidambar styraciflua,* 36; *Rhus copallina,* 24; and such herbaceous species as: *Potentilla canadensis,* 22; *Pycnanthemum flexuosum,* 20; *Solidago nemoralis* and *Lespedeza hirta.*

Very few trees have reached 12 inches DBH. The trees in this area are also more closely spaced, at times almost making dense stands. *Quercus palustris* is no doubt crowded out of areas A and B by other oaks which attain greater height. The whole area is very impressive by its rapidly advancing succession from open field through thicket and bramble stage to climax forest. In seventy years, oak-hickory has regained dominance, now successfully crowding out scrub species.

The position of *Quercus stellata* and *Q. imbricaria* in this Quercus-Carya climax is worthy of note. From Table III it will be seen that *Q. imbricaria* is practically absent in all but the area earliest in succession (Section C) and that *Q. stellata* is relatively abundant in the

TABLE II

Frequency of Species in Fifty Quadrats in Each Area

Species	[1]Area A	Area B	Area C
Carya ovata	100 per cent	86 per cent	68 per cent
C. glabra	76	96	34
Quercus alba	84	90	70
Cornus florida	88	88	94
Fraxinus lanceolata	88	54	62
Quercus velutina	54	80	76
Q. borealis maxima	68	52	40
Prunus serotina	60	74	24
Fraxinus americana	48	54	28
Carya alba	32	56	8
Sassafras variifolium	34	42	36
Diospyros virginiana	34	24	54
Quercus stellata	0	28	48
Juniperus virginiana	4	12	44
Liquidambar styraciflua	2	0	36
Quercus imbricaria	12	12	40
Q. palustris	0	0	30
Acer rubrum	20	4	30
Nyssa sylvatica	26	8	18
Ulmus americana	22	16	14
Rhus copallina	0	2	24
Cercis canadensis	20	14	4
Acer saccharum	16	6	6
Morus rubra	14	10	0
Ulmus fulva	8	10	4
Fraxinus pennsylvanica	8	0	12
Carya cordiformis	6	0	0
Platanus occidentalis	4	0	2
Carya laciniosa	2	0	0
Betula nigra	2	0	0
Juglans nigra	0	4	2
Quercus marylandica	0	2	0
Robinia pseudo-acacia	0	2	2
Liriodendron tulipifera	0	0	16
Prunus americana	0	0	8
Corylus americana	0	0	8
Cratægus sp?	0	0	6
Fagus grandifolia	0	0	4
Acer negundo	0	0	2
Carpinus caroliniana	0	0	2
Quercus bicolor	0	0	2
Total species	27	26	36

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[1] Area A contained virgin timber: Area B was partly cut 55 years ago: Area C entirely cleared 70 years ago.

two stages of succession, but absent in the climax area, which is predominantly *Q. alba* and *Q. velutina* (in so far as Quercus is concerned). It is also worthy of note that *Q. borealis maxima* does not form an important constituent of this Quercus-Carya area in either successional or climax stages.

TABLE III

SHOWING NUMBER OF STEMS OF QUERCUS-SPECIES ONE INCH OR OVER DBH.

SPECIES	SECTION C	SECTION B	SECTION A
Quercus alba	107 stems	111 stems	88 stems
Q. bicolor	1	0	0
Q. borealis maxima	10	8	8
Q. imbricaria	13	1	3
Q. marylandica	0	1	0
Q. palustris	16	0	0
Q. stellata	53	39	0
Q. velutina	48	51	29
Total	248	211	128

TABLE IV

SHOWING NUMBER OF STEMS OF CARYA-SPECIES ONE INCH OR OVER DBH.

SPECIES	SECTION C	SECTION B	SECTION A
Carya alba	1 stems	15 stems	14 stems
C. glabra	20	75	68
C. laciniosa	0	0	1
C. ovata	20	29	105
C. cordiformis	0	0	1
Total	41	119	189

From Tables IV and VI it is seen that all of the Carya-species show greater numbers of stems in the final stage of succession (Section A) than in the earlier successional stage (Section C). *Carya ovata* and *C. glabra* are the chief Carya-components, and *Quercus alba* and *Q. velutina* the chief Quercus-components of this Quercus-Carya climax.

In a general way one might draw the inference that climax forest, reduced to open meadow, will complete the various successional stages in comparatively short time. Shantz (4) found that short grass plains reestablish themselves in twenty to fifty years, and Aikman (1) reports that prairie development requires about thirty or more years to reach the climax from cultivated field condition on Muscatine Island, Iowa. A fair picture of the climax life forms and even of the component species was reached in seventy years in this Indiana area. There are still relics of all the stages in succession, but oak-hickory-ash are showing their dominance by frequency and density. From Table V it will be noted that the total stems of Quercus and Carya over 1 inch DBH. show opposite relationships as the degree of succession advances. The number of Carya stems is over four times as great in the climax stage as in the earliest successional stage, while the number of Quercus stems is almost twice as many in the earliest stage of succession as it is in the climax stage. From this it would appear that Carya-species find a more difficult environment when in competition with so many individuals as are present in earlier stages of succession than they do when in competition with the smaller number of better spaced individuals of the climax, while Quercus-species show the opposite condition.

The same relationship is shown between younger specimens of Carya and Quercus (Table V) in the earliest successional stages and climax. Seedlings of Fraxinus apparently find the habitat more congenial in the climax stage than in the stages of succession. Table V shows over five times as many Fraxinus seedlings in the climax as in the earliest successional stage. From these considerations it would appear that Carya and Fraxinus are both less fitted to the xerophytic conditions of earlier successional stages than some of the Quercus-species. This is also indicated by the apparent high mortality among these species in the young-tree stage when they are in root competition with the mature trees of the climax forest.

The successional stages are characterized by the decreasing total number of species as the climax forest is approached. Lutz (3) found the same feature in the virgin forest at Heart's Content in Pennsylvania, and makes the following conjecture: "This poverty of species may be interpreted as an expression of the ecologically advanced character of the community. As a community advances toward the climax, it tends, more and more, to be composed of a relatively small number of specialized species" (p. 11). This interpretation stands approved by the observational evidence of the present work. Sections A and B are about equal, with twenty-seven and twenty-six species of trees respectively, while Section C, with thirty-six species, has about 33 per cent more than the other sections. This is due to representation of species of successional stages. There is no indication of a beech-maple succession.

This may be due to the physiographic influences of the region, *i. e.*, too rigorous a habitat for them. If beech-maple were the climax here, these species should have come in while Section C was developing.

TABLE V

DENSITY OF CARYA, QUERCUS AND FRAXINUS — BOTH LARGER AND SMALLER SIZE CLASSES, DERIVED FROM FIFTY QUADRATS TEN BY TEN METERS IN EACH SECTION

SIZE RANGE	GENERA	SECTION A	B	C
One inch or over DBH.	Carya	189	119	41
	Quercus	128	211	248
	Fraxinus	83	27	32
Below one inch DBH. 1 meter or over in height	Carya	174	305	83
	Quercus	143	198	240
	Fraxinus	475	150	91

TABLE VII

STEMS OF WOODY SPECIES IN 5,000 SQUARE METERS OF QUADRAT AREA IN EACH SECTION

SIZE RANGE	SECTION A	B	C	TOTAL
Under 1 inch DBH., 1 meter or higher	1207	1059	937	3203
Plants 1-10 inches DBH.	473	429	682	1584
Plants 11-18 inches DBH.	71	47	37	155
Plants 19-32 inches DBH.	34	17	4	55
Total stems over 1 inch	578	493	723	1794
Total stems	1785	1552	1660	4997

Table VI lists number of stems of each woody species under 1 inch DBH. but over 1 meter high. This is summarized and compared with larger stems in Table VII. The final stage of succession shows the largest number of stems under 1 inch and the earliest successional stage shows the smallest number. Stems over 1 inch are largest in number in the earliest stage of succession and smaller in number in the climax area. This is probably due to the fact that the more mesophytic and generally less rigorous habitat of the final stage of succession permits a larger number of seedlings and saplings to get a start than is the case in the earlier successional stage. As growth continues, however, larger percentages of young trees are killed in the struggle for light and water in the final successional stages than in the earlier.

TABLE VI

DENSITY OF WOODY SPECIES BELOW ONE INCH DBH., ONE METER OR OVER IN HEIGHT, DERIVED FROM FIFTY QUADRATS TEN BY TEN METERS IN EACH SECTION

SPECIES	SECTION A	SECTION B	SECTION C
Acer negundo	0	0	2
A. saccharum	6	1	2
A. rubrum	12	2	18
Asimina triloba	5	0	0
Carpinus caroliniana	0	0	4
Carya alba	12	54	3
C. cordiformis	4	0	0
C. glabra	35	119	23
C. ovata	123	132	57
Cercis canadensis	28	21	2
Cornus florida	145	110	155
Corylus americana	7	0	9
Cratægus sp.	0	0	4
Diospyros virginiana	30	20	41
Fagus grandifolia	0	0	2
Fraxinus americana	57	76	5
F. lanceolata	415	74	72
F. pennsylvanica	3	0	14
Juniperus virginiana	2	6	49
Juglans nigra	0	1	1
Liquidambar styraciflua	1	0	35
Liriodendron tulipifera	0	0	2
Morus rubra	16	2	0
Nyssa sylvatica	26	6	9
Prunus americana	0	0	45
P. serotina	96	177	18
Quercus alba	59	59	19
Q. borealis maxima	55	32	21
Q. imbricaria	4	5	45
Q. palustris	0	0	8
Q. stellata	0	38	59
Q. velutina	25	64	88
Rhus copallina	0	1	37
Robina pseudo-acacia	0	2	1
Sassafras variifolium	29	44	70
Ulmus americana	6	8	7
U. fulva	4	5	4
Viburnum acerifolium	1	0	0
V. prunifolium	0	0	4
V. pubescens	1	0	0
Total	1207	1059	937

SUMMARY AND CONCLUSIONS

1. The Mauntel woods in Dubois county, Indiana, is a typical oak-hickory association.

2. Both areas of secondary succession are reverting to the oak-hickory climax.

3. The earliest successional stage is outstanding in its greater number of species and presence of relics from earlier successional stages.

4. There appears to be little difference between reproduction in virgin forest and adjacent areas of secondary succession.

5. Indications are that very large trees were the unusual rather than the common occurrence in the forest primeval. Oak seems to have been most common between 24-32 inches DBH. in mature stands.

6. Reproduction in virgin timber apparently is a matter of occupying vacated territory rather than a continuous growth of young trees under the crowns of a mature stand.

7. *Quercus stellata* and *Q. imbricaria* are characteristic of earlier successional stages, but are essentially absent from the final stage.

8. Carya-species are few in number of stems in earlier successional stages, but form a prominent part in the forest of the final stage.

9. The chief components of the oak-hickory climax here studied are *Q. alba, Q. velutina, C. glabra* and *C. ovata.*

10. Mortality appears to be high in the case of Fraxinus.

11. *Cornus florida* is the only second-layer tree of any consequence.

12. There are no indications that beech-maple association will succeed the oak-hickory association in the area studied.

Our sincere thanks are here expressed to Mr. Mauntel for scientific foresight in preserving the area here under study and for his kindness in permitting our work to be done on it.

LITERATURE CITED

1. AIKMAN, J. M. Secondary plant succession on Muscatine Island, Iowa. Ecology 11:577-588. 1930.
2. CAIN, STANLEY A. Studies of virgin hardwoods forest I: Density and frequency of the woody plants of Donaldson's woods, Lawrence county, Indiana. Proc. Indiana Acad. Sci. 41:105-122. 1932.
3. LUTZ, H. J. The vegetation of Heart's Content, a virgin forest in northwestern Pennsylvania. Ecology 11:1-29. 1930.
4. SHANTZ, H. L. Plant succession on abandoned roads in eastern Colorado. Jour. Ecology 5:19-42. 1917.

ADDITIONS TO THE ALGAL FLORA OF MARION COUNTY, INDIANA

By Charlene Coffing

In January, 1933, the writer began working on a special problem in the identification of the plankton algæ of the canal which cuts through the Butler University campus. The primary purpose of the problem is the study of the periodicity of the algæ of the canal. It is planned to consider in a later paper this study of periodicity which will include both seasonal and weekly variations which occurred in the kinds of algæ and the effect of temperature of water and amount of precipitation upon the algal flora.

From January 30 to October 30 the algæ from forty samples of water were identified. It is hoped that the later paper on periodicity will include fifty-two samples, a sample being taken once a week at regular intervals.

In the forty samples, 146 species and varieties have been identified. Of this number, seventy-three have not been reported previously for Marion county. Forty-six of the forms new for the county are also new for Indiana. A list of the species and varieties new for Marion county is included in this report. The forty-six forms which have not been reported previously for Indiana are in boldface type. The list includes forty-three genera and sixty-seven species and varieties. Fifteen of the genera reported are new for Marion county, while six of this number have not been reported before for the state. The six genera which are new for the state are: Botrydiopsis?, Frustulia?, Hemidinium, Phacotus, Quadrigula, Schrœderia.

When the identification has been uncertain, a question mark is placed after the name of the alga.

The algæ are grouped according to classes, the classification being based on that used by Smith.[1]

The writer wishes to express her appreciation to Professor C. Mervin Palmer, who suggested and directed this problem.

The algæ which have not been reported previously for Marion county are as follows:

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[1] Smith, Gilbert M. The Fresh-water Algæ of the United States. 1 Ed. 1933.

MYXOPHYCEÆ

Anabæna spiroides Klebahn
Cœlosphærium Kuetzingianum Näg.
Lyngbya contorta Lemm.

HETEROKONTÆ

Botrydiopsis?
Ophiocytium capitatum Wolle var. longispinum (Möbius) Lemm.

CHRYSOPHYCEÆ

Dinobryon sertularia Ehr.

BACILLARIEÆ

Asterionella formosa Hass.
Cymbella prostrata (Berk.) Cleve
C. ventricosa Kütz.
Eunotia lunaris (Ehr.) Grun.
Frustulia rhomboides (Ehr.) DeToni?
Gomphonema olivaceum (Lyngb.) Kütz.
G. parvulum (Kütz.) V. H.
Gyrosigma sp?
G. Kuetzingii (Grun.) Cleve
G. scalproides (Rab.) Cleve
Meridion circulare (Grev.) Ag.
Navicula cuspidata Kütz.
N. radiosa Kütz.
N. rhyncocephala Kütz.
Nitzschia acicularis (Kütz.) W. Smith
N. acicularis (Kütz.) W. Smith var. closterioides Grun.
N. amphibia Grun.
N. clausii Hantzsch
N. palea (Kütz.) W. Smith?
N. parvula W. Sm.?
N. vermicularis (Kütz.) Hantzsch
Pinnularia sp?
P. brebissonii (Kütz.) Cleve
P. divergens W. Smith?
P. subcapitata Greg. var. paucistriata Grun.
P. sublinearis (Grun.) Cleve
Stauroneis anceps Ehr.
S. phœnicenteron (Nitzsch) Ehr.
Synedra acus Kütz.
S. parvula Kütz.
S. pulchella (Ralfs) Kütz.
S. ulna (Nitzsch) Ehr.

CHLOROPHYCEÆ (EXCLUDING DESMIDS)

Ankistrodesmus falcatus (Chorda) Ralfs var. mirabilis (W. & G. S. West) G. S. West
Carteria
Chlorella variegatus Beyerinck?
Crucigenia fenestrata Schmidle
Glœocystis gigas (Kütz.) Lagerh.
Golenkinia radiata Chod.
Kirchneriella lunaris (Kirchner) Möb.
K. obesa (W. West) Schmidle
K. obesa (W. West) Schmidle var. major (Bernard) G. M. Smith
Lagerheimia ciliata (Lagerh.) Chod.
L. longiseta (Lemm.) Printz
L. subsala Lemm.
L. wratislawiensis Schröder
Nephrocytium limneticum G. M. Smith
Œdogonium
Oocystis parva W. & G. S. West
Phacotus lenticularis (Ehr.) Stein
Quadrigula lacustris (Chod.) G. M. Smith
Scenedesmus bijuga (Turp.) Lagerh. var. alternans (Reinsch) Borge
Schrœderia judayi G. M. Smith
S. setigera (Schröder) G. M. Smith
Selenastrum gracile Reinsch
Tetrastrum elegans Playfair
Treubaria setigerum (Archer)
T. triappendiculata Bernard

DESMIDIACEÆ

Closterium venus Kützing?
Cosmarium sp?

DINOPHYCEÆ

Ceratium hirundinella (O. F. M.) Schrank
Hemidinium nasutum Stein

ENGLENOPHYCEÆ

Englena intermedia (Klebs) Schmitz
E. intermedia (Klebs) Schmitz var. **klebsii** Lemm.
Phacus anacœlus Stokes
P. orbicularis Hübner
Trachelomonas acuminata (Schmarda) var. **verrucosa** Teodor.
T. volgensis Lemm.?

ALGÆ OF STEUBEN COUNTY, INDIANA. I

By C. MERVIN PALMER

No published record has yet been made, apparently, of the algal flora of Steuben county, Indiana. The many lakes and bogs, together with several streams which are in the county, make the area an excellent one for collecting algæ. The writer visited the county in May, 1929, July and September, 1933, and obtained specimens particularly from the following lakes: Bass, Crooked, Failing, Fox, Hogback, James, Nevada Mills and Snow. Approximately fifty algæ have so far been identified from the collections. Those that have not previously been reported for Indiana are printed in boldface type. It is hoped that additional lists of the algæ of Steuben county may be published from time to time. No desmids or diatoms are included in this first paper.

MYXOPHYCEÆ

Anabæna spiroides Klebahn; Hogback L., July. The straight species has not been reported previously for Indiana. Variety "crassa" was reported for Vigo county.

Aphanothece stagnina (Spreng.) A. Br.; Crooked L., Sept. Specimens differ from the species description in having several pseudovacuoles present in each cell.

Calothrix **castellii** (Mass.) B. and F.; L. James, Sept.

Chroococcus **minutus** (Kütz.) Näg.; L. at Nevada Mills, Sept.

Chroococcus turgidus (Kütz.) Näg.; Crooked L., Sept.

Chroococcus **turicensis** (Näg.) Hansgirg; Crooked L., Sept. Cells 18-30 microns in diameter, brownish, granular; probably rare for the United States.

Cœlosphærium nægelianum Unger; Hogback L., July.

Glœotrichia echinulata (J. E. Smith) P. Richter; Crooked L., Sept.

Gomphosphæria aponina Kütz.; Crooked L., Sept.

Gomphosphæria lacustris Chod.; Fox L., July.

Lyngbya ærugineo-cœrulea (Kütz.) Gom.; stream east of Snow L., Sept.

Lyngbya **birgei** G. M. Smith; Fox L., July. Resembles L. **hieronymusii** Lemm. but specimens are too large for that species. Filament 27 microns in diam.; trichome 18 microns in diam. Cells 2.5-3 microns long.

Lyngbya **majuscula** (Dillw.) Harvey; stream east of Snow L., Sept. The largest species of Lyngbya, generally marine, but sometimes found in fresh water. Specimens studied had the following dimensions: diam. filament 46-61 microns; diam. trichome 36-43 microns; sheath thickness 5-10 microns; cell length 3.6-7.2 microns. Cells were green, blue and purplish-blue (preserved in weak formalin).

Merismopedia glauca (Ehr.) Näg.; stream east of Snow L., Sept.

Merismopedia tennuissima Lemm.; Fox L., July.

Nostoc pruniforme Ag.; Bass L., July.
Oscillatoria geminata Menegh.; Failing L., July.
Phormidium **ambiguum** Gomont; small pond in Pokagon Park.
Phormidium retzii (Ag.) Gomont; stream east of Snow L., Sept.
Rivularia **globiceps** G. S. West; Failing L., July.
Spirulina major Kütz.; lake at Nevada Mills, Sept.
Stigonema informe Kütz.; lake at Nevada Mills, Sept.
Tolypothrix lanata Wartm.; Hogback L., July. On Chara.
Tolypothrix tenuis Kütz.; Crooked L., Sept.

Chlorophyceæ (and All Algæ Other Than Myxophyceæ)

Ankistrodesmus falcatus (Corda) Ralfs; Failing L., July.
Aphanochæte repens A. Br.; Crooked L., Sept.
Bulbochæte **monile** Wittr. and Lundell, var. **robusta** Hirn.; Bass L., July.
Chara **delicatula** Agardh., var. **annulata** (Wallman) G. and B. W.; Crooked L., Sept. A small form growing in shallow water along the shore line.
Chara fragilis Desvaux; Bass L. and bog near Hogback L., July.
Chlorococcum humicola (Näg.) Rab.; on cow manure in boggy area near Snow L., Sept.
Cladophora crispata (Roth.) Kütz.; Hogback L., July.
Cœlastrum microporum Näg.; lake at Nevada Mills, Sept.
Cylindrocapsa geminella Wolle; Crooked L., Sept. Rare for the U. S.
Euglena spirogyra Ehrenb.; bog, May.
Glœotænium loitlesbergerianum Hansg.; Bass L., July. Colony of four cells; length of colony 47 microns, width 42 microns.
Hydrodictyon reticulatum (L.) Lagerh.; pond west of Snow L., Sept.
Kirchneriella obesa (W. west) Schmidle; Crooked L., Sept.
Nitella tenuissima Kütz.; Bass L., July.
Pandorina morum Bory; bog north of Snow L., Sept.
Pediastrum boryanum (Turp.) Menegh.; Hogback L., July.
Pediastrum tetras (Ehr.) Ralfs; bog north of Snow L., Sept.
Phacus pleuronectes (Müll.) Duj.; bog north of Snow L., Sept.
Radiofilum **conjunctivum** Schmidle; Bass L., July. Helmet-shaped segments of wall present. Cell diam. 4.5-5.5 microns; cell length 5-6.5 microns. No gelatinous sheath visible in some of the specimens.
Scenedesmus arcuatus Lemm., var. platydisca G. M. Smith; in drinking trough, July.
Scenedesmus bijuga (Turp.) Lag.; bog north of Snow L., Sept., and lake at Nevada Mills, Sept.
Scenedesmus **brasiliensis** Bohlin; Failing L., July.
Scenedesmus obliquus (Turp.) Kütz.; drinking trough, July.
Sphærocystis schrœteri Chod.; lake at Nevada Mills, Sept.
Trachelomonas **acanthostoma** Stokes; bog north of Snow L., Sept. Short, rough collar; short spines on anterior end of cell.
Tribonema **utriculosum** (Kütz.) Hazen; swamp, May.

THE SHRUBS OF INDIANA IN THEIR LOCAL AND GENERAL DISTRIBUTION ACCORDING TO PHYSIOGRAPHIC DIVISIONS

By Lettie Page Trefz

The mesophytic deciduous forest is the climax type of flora in Indiana. The trees typify the dominant life-form of such a community, but the shrubs and herbaceous plants which go to make up the undergrowth have an important bearing on the nature of the vegetation as a whole. Within each climax formation there are numerous physiographic areas in which differences in vegetation are associated primarily with differences in topography and soil character. In Indiana there are six such areas, each with its distinctive floras (6, 11, 15). Lindsey (12) has made a study of the trees of Indiana, dealing with their distribution within the state in natural botanical areas and outside the state in their wider distribution by larger physiographic units. The present paper involves a study of the shrubs following the manner of the study of trees made by Lindsey.

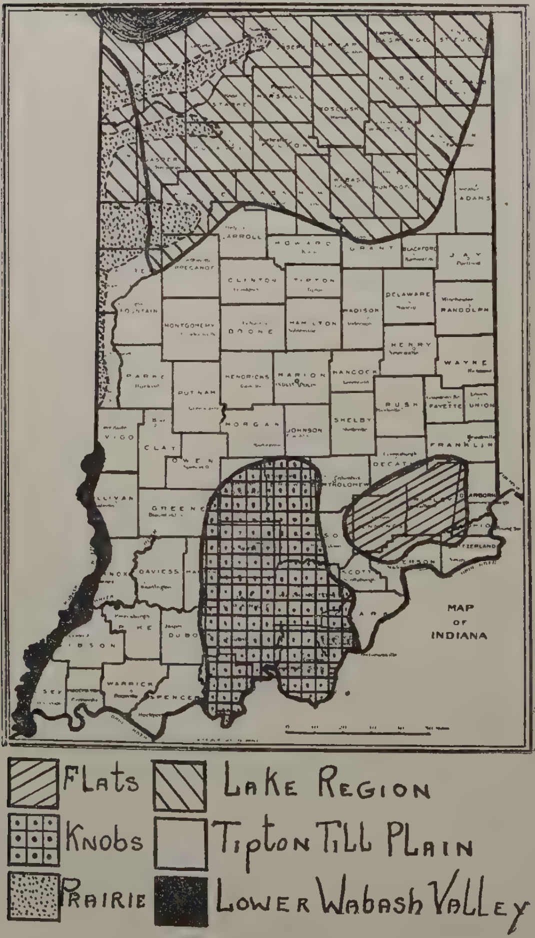
LOCAL AND GENERAL DISTRIBUTION

The shrubs of Indiana listed are the 212 species, varieties and forms vhich Deam (8) recognizes as occurring outside of cultivation within he state. Their distribution follows the ranges fixed by Deam, supplenented by the Butler University Catalogue of Indiana Plants, which ecords by counties all published records for each species. Where the ange of a species has been enlarged to include more botanical areas than hose given by Deam, it is starred and the collector given credit in a footiote (Table I). The nomenclature used is that of Deam's second edition f the Shrubs of Indiana. Whenever a conflict exists among workers conerning either the taxonomy or distribution of a species, the authority of eam is given precedence. Since Indiana is divided into ninety-two counies and since these counties fall into six major botanical areas as indicated y Deam (7, 8), the local range of a species is determined first by counties nd afterwards by botanical areas.

On the basis of the facts concerning the topography and geology of ndiana, Coulter and Thompson (3) divided Indiana into seven botanical egions. Deam (6) differentiated the botanical areas of Indiana according to habitats having distinctive floras. In his later works (7, 8), he has delimited six well marked forestal areas in Indiana, modifying in some respects the divisions of Coulter and Thompson and his own earlier subdivision. Since these forestal areas have been followed in this study. Map 1 shows the outline of each area.

MAP 1

DEAM'S BOTANICAL AREAS OF INDIANA



DISTRIBUTION BY BOTANICAL AREAS

Maps were prepared which showed county distribution of the 212 species, and from these a list of the species occurring in each of Deam's botanical areas was prepared. Table I gives the location of species by botanical areas, the number of species in each area and the percentage in each area of the total number of shrubs found in the state.

TABLE I

Shrubs of Indiana and Their Location by Botanical Areas

Name of Species	Region of Location[1]						
	AA	L	TP	P	LWV	K	F
Alnus rugosa (Du Roi) Sprengel		x	x			x	
Amelanchier humilis Wiegand		x					
A. humilis x Amelanchier lævis Wiegand		x					
Amorpha canescens Pursh		x	x	x			
A. fruticosa L.		x	x		x	x	
Ampelopsis cordata Mx.			x		x	x	
Andromeda glaucophylla Link		x					
Aralia spinosa L.			x			x	x
Arctostaphylos uva ursi var. coactilis Fernald and MacBride		x					
Aristolochia tomentosa Sims					x		
Aronia floribunda (Lindley) Spach		x	x				
A. melanocarpa (Mx.) Ell.		x	x			x	x
Ascyrum hypericoides L.			x			x	
Benzoin æstivale (L.) Nees	x						
Betula pumila L.		x					
B. pumila var. glandulifera Regel		x					
XB. purpusii Schneider		x					
Bignonia capreolata L.					x	x	
Bumelia lycioides (L.) Gaertn.						x	
Campsis radicans (L.) Seemann	x						
Ceanothus americanus L.	x						
C. ovatus Desf.		x					
Celastrus scandens L.	x						
Celtis pumila var. deamii Sarg.						x	
Cephalanthus occidentalis L.	x						
[2]C. occidentalis var. pubescens Raf.		x	x		x	x	
Chamædaphne calyculata (L.) Moench		x					
Cornus alternifolia L. f.	x						

[1] Explanation of column headings: AA, All Areas; L, Lake Area; TP, Tipton Till Plain; P, Prairie Area; LWV, Lower Wabash Valley Area; K, Knobs Area; F, Flats Area.

[2] Peattie (17) extends the range of this species in Indiana into the Lake Area.

NAME OF SPECIES	AA	L	TP	P	LWV	K	F
C. amomum Mill.			x			x	
C. asperifolia Mx.	x						
C. baileyi Coulter and Evans		x					
C. obliqua Raf.	x						
C. racemosa Lam.	x						
C. rugosa Lam.		x	x				
C. stolonifera Mx.		x	x				
C. stricta Lam.			x		x	x	
Corylus americana Walter	x						
Cratægus alnorum Sarg.		x					
C. arduenna Sarg.		x					
C. barrettiana Sarg.			x				
C. brainerdi Sarg.		x					
C. conjuncta Sarg.		x					
C. dewingii Sarg.			x				
C. erecta Sarg.			x				
C. gracilis Sarg.			x				
C. gracillipes Sarg.		x					
C. hillii Sarg.			x				
C. ignea Sarg.		x					
[3]C. intricata Lange		x	x				
C. meticulosa Sarg.						x	
C. palustris Ashe			x				
C. parviflora Sarg.		x					
C. rotundifolia Moench.		x					
C. rutila Sarg.		x					
C. sejuncta Sarg.		x					
C. spathulata Mx.					x		
C. straminea Beadle		x					
C. trahax Sarg.			x				
Diervilla lonicera Mill.		x	x				
Dirca palustris L.		x	x			x	x
Epigæa repens L.		x	x			x	
Evonymus americanus L.						x	x
E. atropurpureus Jacq.	x						
E. obovatus Nutt.		x	x	x		x	x
Gaultheria procumbens L.		x	x			x	
Gaylussacia baccata (Wang.) K. Koch		x	x			x	x
G. baccata var. leucocarpa (Porter) Fernald		x	x				
Grossularia cynosbati (L.) Mill.		x	x	x		x	x
G. hirtella (Mx.) Spach		x					
G. missouriensis (Nutt.) Coville and Britton		x	x			x	x
Hamamelis virginiana L.	x						

The header "REGION OF LOCATION" spans columns AA through F.

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[3] Range extended into the Lake Area by a report of Peattie (17).

Name of Species	Region of Location						
	AA	L	TP	P	LWV	K	F
Hudsonia tomentosa var. intermedia Peck		x					
Hydrangea arborescens L.	x						
H. arborescens var. deamii St. John			x		x	x	
H. arborescens var. oblonga T. and G.	x						
Hypericum kalmianum L.		x					
H. prolificum L.	x						
Ilex decidua Walter			x		x		
I. verticillata (L.) Gray	x						
Juniperus communis var. depressa Pursh		x	x				
Kalmia latifolia L.						x	
Lonicera canadensis Marsh.		x					
L. dioica L.		x					x
L. dioica var. glaucescens (Rydberg) Butters		x	x				
L. dioica var. glaucescens forma dasygna (Rehder) Deam		x				x	x
L. japonica Thunb.			x			x	x
L. prolifera (Kirchner) Rehder		x	x				
Myrica asplenifolia L.		x					
Nemopanthus mucronata (L.) Trel.		x					
Parthenocissus quinquefolia (L.) Planchon	x						
[4]P. vitacea (Knerr) Hitchc.		x	x			x	
Phoradendron flavescens (Pursh.) Nutt.					x	x	x
Physocarpus opulifolius (L.) Maxim.	x						
P. opulifolius var. intermedius (Rydberg) Robinson		x					
Potentilla fruticosa L.		x	x				
Prunus angustifolia Marsh.		x	x			x	x
P. pumila L.		x					
P. virginiana L.		x	x			x	x
P. virginiana var. demissa (Nutt.) Torr.		x	x				
Ptelia trifoliata L.	x						
P. trifoliata var. deamiana Nieuwland		x					
P. trifoliata forma mucronata (Nieuwland) Deam		x					
Rhamnus alnifolia L'Heriter		x					
R. caroliniana Walt.						x	
R. caroliniana var. mollis Fernald						x	
R. lanceolata Pursh.		x	x			x	
Rhus canadensis Marsh.		x	x			x	x
R. copallina L.	x						
R. glabra L.	x						
R. glabra var. borealis Britton		x					
R. toxicodendron L.	x						
R. typhina L.		x	x		x		
R. vernix L.		x	x		x	x	

[4] Price and Welch (19) report this species for Monroe County, which extends it into the Knobs Area.

NAME OF SPECIES	REGION OF LOCATION						
	AA	L	TP	P	LWV	K	F
Ribes americanum Mill.	x						
R. americanum var. mesochora Nieuwland		x					
Rosa blanda Ait.		x	x				
R. blanda var. glandulosa Schuette		x					
R. blanda var. hispida Farwell		x					
R. carolina L.	x						
[5]R. carolina var. glandulosa (Crepin) Farwell		x	x			x	
R. carolina var. sabulosa Erlanson		x					
R. deamii Erlanson				x			
R. lyoni Pursh.	x						
R. obovata Raf.		x	x				
R. palustris Marsh.	x						
R. relicta Erlanson				x			
R. rubiginosa L.		x	x		x	x	
R. rudiuscula Greene				x			
R. setigera Mx.	x						
R. setigera var. tomentosa T. and G.	x						
R. suffulta Greene				x			
Rubus allegheniensis Porter	x						
R. alumnus Bailey		x			x		
R. argutus Link	x						
R. flagellaris Willd.	x						
R. frondosus Bigel.	x						
R. hispidus L.		x	x				x
R. hispidus forma pleniflorus Nieuwland		x					
R. idæus var. canadensis Richardson		x					
R. idæus var. strigosus (Mx.) Maxim.		x					
R. occidentalis L.	x						
R. occidentalis forma pallidus (Bailey) Robinson		x	x				
R. odoratus L.			x			x	
Salix adenophylla Hook.		x					
S. bebbiana Sarg.		x	x				
S. candida Flügge		x					
S. candida var. denudata Andersson		x					
S. cordata Muhl.		x	x	x			x
S. discolor Muhl.	x						
S. discolor var. eriocephala (Mx.) Andersson	x						
S. glaucophylla Bebb		x					
S. humilis Marsh.	x						
S. longifolia Muhl.	x						
S. longifolia var. wheeleri (Rowlee) Schneider		x	x			x	
S. longipes Shuttleworth						x	
S. lucida Muhl.		x					

[5] Range extended into the Lake Region by a report of Peattie (17).

NAME OF SPECIES	REGION OF LOCATION						
	AA	L	TP	P	LWV	K	F
S. lucida var. intonsa Fernald		x					
S. pedicellaris Pursh.		x	x				
S. petiolaris J. E. Smith		x	x				
S. sericea Marsh.		x	x		x	x	x
S. serissima (Bailey) Fernald		x					
S. tristis Ait.		x	x	x		x	
Sambucus canadensis L.	x						
S. canadensis forma atroflavula House		x					
S. pubens Mx.		x	x				
S. pubens var. zanthocarpa Nieuwland		x					
Shepherdia canadensis (L.) Nutt.		x					
Smilax bona-nox L.						x	
S. glauca Walt.			x		x	x	x
S. hispida Muhl.	x						
S. rotundifolia L.	x						
Sorbus subvestita Greene		x					
Spiræa alba DuRoi	x						
S. tomentosa L.		x	x	x			x
Staphylea trifolia L.	x						
Styrax americana Lam.		x			x	x	
Symphoricarpos orbiculatus Moench			x		x	x	x
Taxus canadensis Marsh.			x				
Vaccinium arboreum Marsh.						x	
[6]V. canadense Kalm		x	x				
V. corymbosum L.		x					
V. corymbosum var. amœnum (Ait.) Gray		x					
V. corymbosum var. atrocarpum Gray		x					
V. corymbosum var. pallidum (Ait.) Gray		x					
V. macrocarpon Ait.		x	x				
V. oxycoccus L.		x					
V. pennsylvanicum Lam.		x					
V. pennsylvanicum var. nigrum Wood		x					
V. stamineum L.			x			x	x
V. stamineum var. neglectum (Small) Deam						x	
V. vacillans Kalm		x	x			x	x
V. vacillans var. crinitum Fernald		x	x			x	
Viburnum acerifolium L.		x	x			x	x
V. acerifolium forma ovatum Rehder							x
V. affine Bush		x	x				
V. affine var. hypomalacum Blake		x	x				
V. cassinoides L.		x					
V. lentago L.	x						
V. molle Mx.			x				x

[6] Range extended into the Lake Area by a specimen in the Butler University Herbarium.

Name of Species	Region of Location						
	AA	L	TP	P	LWV	K	F
V. prunifolium L.	x						
V. pubescens var. deamii Rehder			x			x	x
V. pubescens var. indianense Rehder			x			x	x
V. rufidulum Raf.						x	x
V. trilobum Marsh.		x					
Vitis æstivalis Mx.	x						
V. cinerea Engelm.		x	x		x	x	
V. cordifolia Mx.	x						
V. labrusca L.		x	x		x		x
V. rubra Mx.					x		
V. vulpina L.	x						
[7]V. vulpina var. syrticola Fernald and Wiegand		x	x				
Zanthoxylum americanum Mill.	x						
Total species per area	48	119	78	10	21	55	30
Per cent per area of the 212 total shrubs	23	56	37	5	10	26	14
Per cent per area of the 163 total trees of Indiana—Lindsey (12)	10	71	65	14	66	65	45

To this list of shrubs for Indiana by Deam (8), other authors have added species (13, 17, 18). Some of these species are: *Hamamelis virginiana orbiculata* Nieuwland, *Hudsonia tomentosa* Nutt, *Rubus floricomus* Blanchard, *R. idaeus* var. *anomalus* Arrhenius, *R. randii* (Bailey) Rydberg, *R. recurvans* Blanchard, *Vaccinium atrococcum* (Gray) Heller and *V. corymbosum* var. *glabrum* Gray. Since these shrubs either are not included or given specific rank by Deam, they are omitted from the list for this discussion. Recently, a new shrub, *Rubus phoenicolasius* Maxim, was collected in Crawford county and added to the Butler University Herbarium. This species has been introduced into America from Japan and is an escape in Crawford county. However, it is becoming established in open places on the hills near Marengo Cave and in time may be added to our Indiana flora.

Deam (8) has excluded sixty-eight species of shrubs from the Indiana list for want of satisfactory evidence to warrant their inclusion. Of these, some have ranges far beyond our area, some have been reported as escapes, and the reports on others have been too indefinite. The species of Berberis, injurious to wheat by the black stem rust, have been excluded because these shrubs will not become members of our flora since an effort is being made to exterminate them. For a further discussion of the excluded species, reference should be made to Deam (8).

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[7] Range extended into the Tipton Till Plain by a specimen from Parke County in the Butler University Herbarium.

Table I shows that the Lake area has the highest number of shrub-species of any of the areas, due no doubt to the unusual number of Lake region exclusives and to the fact that many of the species occurring in one or more of the other areas occur also in the Lake region.

The Tipton Till Plain follows in the number of species it possesses, while the Knobs, Flats, Lower Wabash Valley and Prairie areas follow with decreasing percentages. A comparison of the shrubs with the trees is given in percentages at the end of Table I. It is seen that the tree species of Indiana occur in the largest numbers also in the Lake area, while the Lower Wabash Valley, the Tipton Till Plain and Knobs, the Flats and the Prairie areas follow with decreasing percentages. It is interesting also to note that 23 per cent of the shrub species and only 10 per cent of the tree species occur in all areas.

From the figures the Prairie region would appear to be practically shrubless until it was remembered that species listed for all areas occur in the Prairie region also. Welch (28) has made a study of one of the prairie counties and finds that these areas in Indiana are in the transition zone between deciduous forest and prairie. The prairie type of vegetation is decidedly dominant, but trees and shrubs are found in groves in habitats supplied with sufficient water for their maintenance and in situations high enough to have been protected from the annual prairie fires. The Lower Wabash Valley region is also limited in species, due to the fact that this is a very narrow strip of land subject to inundation by the Wabash river. Such an area naturally would contain only those species which could adjust themselves to such a variable habitat.

These numerical values of the regions are not absolute, because areas are not sharply defined. A species may be found plentifully in one area, but it may be able to survive across the boundary of its characteristic area, and even though only a few shrubs of this species exist in this contiguous area, it is counted in both areas. Where shrubs occur only in counties near the border-line of an area, it is difficult to determine whether they should be placed in one or both areas. This was especially true of the Cratægi. Such a small amount of information could be gleaned concerning their habitats that it was difficult to decide in a number of cases whether a species belonged in the Lake region or in the Tipton Till Plain. If a more accurate distribution were possible, it is certain that there would be changes in these figures. Deam (6) has pointed out, "The number of plants found in a state depends largely upon the intensity with which they are sought." This, no doubt, is true of the shrubs in the different botanical areas. In all of the areas there are species either exclusive or characteristic of the area.

THE LAKE REGION

In Table I it will be noted that sixty species are limited to the Lake area. This region contains more exclusives than all other areas combined. The general distribution of all these species has not been worked out by any one, but the known wider distribution of these exclusives is characteristically extraneous to the north, northwest and northeast, although some have western and some have eastern and southeastern extensions along the Appalachians. Three species, *Ribes americanum* var. *mesochora*, *Rubus hispidus* forma *plentiflorus* and *Sambucus pubens* var. *xanthocarpa* have no distribution reported except that for the immediate vicinity of the Lake region in Indiana.

Most of these shrubs find the bogs, swamps and sand dunes suitable habitats, while a number find the open woods of this area a suitable environment. Of the 51 shrubs whose habitats have been noted by collectors, 51 per cent prefer the swamps and bogs, 31 per cent the sand dunes, while 33 per cent are found in open woods. Of those found in the open woods, 14 per cent are found also in the bogs, swamps or sand dunes. The species found in the extreme habitats of bog, swamp and sand dunes may linger here at the southern edge of their range until their position is no longer tenable, due to the invasion of the oaks and the climax forests into these habitats (4, 5).

KNOBS AREA

Of the fifty-five species of shrubs found in the Knobs area in the unglaciated region in Indiana, ten were found to be exclusive to the area (Table I).

The wider distribution of the shrubs of this area is heaviest toward the south and southeast. Plants preferring a southern habitat can be found in this region in the warm protected ravines. However, *Kalmia latifolia* is restricted to the ledges and upper parts of the ridges in the Knobs area. This species is found nowhere else in Indiana, but it shows an affinity for the far northeast in its wider distribution. This gives evidence that both here and in eastern and southeastern mountains, conditions characteristic of more northern areas apparently pertain. In this area, then, plants preferring either a cooler or a warmer climate find a suitable environment. Coulter and Thompson (3) state that the plants of this region are peculiar in that species on one side of a knob may be found growing in a climate similar to that of Northern British America, while on the other side of the same knob plants may be found flourishing luxuriantly whose natural climate is found in Florida or Mississippi.

THE LOWER WABASH VALLEY AREA

The Lower Wabash Valley region is less distinctive than either the Lake or Knobs areas in the number of exclusives possessed. Of the twenty-one shrubs listed for the Lower Wabash Valley, only four are exclusive, *viz.*, *Aristolochia tomentosa*, *Crataegus spathulata*, *Vitis rubra* and *Foresteria acuminata*. This latter species often appears as a small tree, but in Indiana it is usually shrublike. No doubt the shrubs of this region have found here a climate very similar to that of southern latitudes in the low grounds and protected ravines, since most of them find the lowlands a suitable habitat. They are southern, southeastern and southwestern in their general ranges.

The Lake region exclusives are on the southern limit of their ranges in northern Indiana. The Knobs and Lower Wabash Valley exclusives are on the northern limit of their ranges in southern Indiana. Cowles (5) states that the behavior of species at the edge of their ranges may be regarded as extremely significant of the present trend of migration. The exclusives of these areas seem to indicate that the shrubs, like the trees, are entering Indiana from the south and southeast and are leaving by the north and northeast (12).

THE FLATS AREA

The Flats area is less distinctive in regard to its shrub flora than any of the other areas, since it possesses no exclusive species.

THE TIPTON TILL PLAIN

Seven species of Cratægus are listed as exclusives of the Tipton Till Plain. These species are reported for only one county each and most of them for counties so near the boundary between regions that it is difficult to ascertain to which region each species really belongs. When more reports have been made on these species, it may be found that they are not all Tipton Till Plain exclusives. Little is known about their general distribution.

Taxus canadensis is a glacial relic and is exclusive to this area. It is found only in Montgomery and Parke counties in Indiana and grows usually under hemlock trees or near them. While it is geographically exclusive to this area, its physiographic relations are not at all characteristic of the physiography of the area.

THE PRAIRIE AREA

The Prairie area is distinctive in having the smallest percentage of shrubs of any botanical area. There are four exclusive species: *Rosa deamii, R. relicta, R. rudiuscula* and *R. suffulta*. *R. relicta* and *R. suffulta* are not found in the Prairie as this area is delimited on Map 1, but they are considered as Prairie exclusives because they occupy prairie habitats in Indiana and have been reported in no other environment in this state. *Rosa rudiuscula* and *R. suffulta* are on the eastern limit of their ranges in the Prairie area in Indiana. *R. suffulta* extends throughout the western prairies, while *R. rudiuscula* is extraneous to the southwest. The general distribution of *R. deamii* and *R. relicta* is not known.

SPECIES WITH RANGE LIMITS IN INDIANA AND WHICH OCCUPY MORE THAN ONE BOTANICAL AREA IN INDIANA

Of the shrubs exclusive to different botanical areas of Indiana, those of the Knobs area range over the most restricted territory, while those characteristic of Tipton Till Plain and Prairie areas range over the most extensive territory. The great majority of Indiana shrubs are intraneous in varying degrees in their wider distribution, but the species with verified range limits listed in the tables as being exclusive to an area are extraneous. Other species having ranges which terminate in Indiana, but which are not confined to a single botanical area, are given in Table II.

TABLE II

SPECIES WHICH OCCUPY MORE THAN ONE BOTANICAL AREA IN INDIANA AND WHOSE RANGES TERMINATE IN INDIANA

NAME OF SPECIES	DIRECTION OF GENERAL DISTRIBUTION							
	N	E	NE	NW	W	S	SE	SW
Amorpha canescens				x	x	x		x
Ampelopsis cordata		x			x	x	x	x
Aralia spinosa		x				x	x	x
Aronia floribunda	x	x	x	x			x	
A. melanocarpa	x	x	x	x			x	
Ascyrum hypericoides		x			x	x	x	x
Bignonia capreolata		x				x	x	
Cephalanthus occidentalis var. pubescens						x		x
Cornus rugosa	x	x	x	x				
C. stricta		x				x	x	x
Cratægus intricata		x	x		x		x	
Diervilla lonicera	x	x	x	x			x	
Evonymus americanus		x	x		x	x	x	x
Hydrangea arborescens		x			x	x	x	
H. arborescens var. deamii		x			x	x		x
H. arborescens var. oblonga		x			x	x	x	
Ilex decidua		x			x	x	x	x
Juniperus communis var. depressa	x	x	x	x	x			
Parthenocissus vitacea	x	x	x	x	x			x
Phoradendron flavescens		x				x	x	x
Potentilla fruticosa	x	x	x	x	x			x
Rosa blanda	x	x	x	x	x			
Rubus alumnus					x			
R. odoratus		x	x				x	
Salix bebbiana	x	x	x	x	x			
S. longifolia var. wheeleri	x	x	x	x	x			
S. pedicellaris	x	x	x	x				
Sambucus pubens	x	x	x	x	x		x	
Smilax glauca		x	x		x	x	x	x
Styrax americana		x				x	x	
Viburnum molle		x			x	x	x	x
V. rufidulum		x			x	x	x	x
Vitis cinerea					x		x	x
Total (33)	12	29	16	13	21	17	21	16

MIGRATION, RELICS, ENDEMICS, DISJUNCTS AND COASTAL PLAIN SPECIES

During the past, successive waves of vegetation have passed over Indiana, due to the advance and retreat of the glaciers. Since the state lies in the central northern part of the country, it became the common meeting ground of postglacial migrations from various directions. Many warmth-loving plants were able to migrate before the cold, which came on gradually, while those of higher latitudes were driven in to take their places. With the return of warmer conditions, the ice cap retreated, permitting and compelling plants to move northward again. In these alternate movements, which may have taken place several times, relic species have been stranded in our present flora. Some of these are listed in Table III.

A number of species of Atlantic Coastal Plain affinity found a more or less continuous pathway for inland extension during this time. These plants may have migrated from three different sources: the Mississippi basin, from the Mohawk-Hudson outlet and the eastern Great Lakes, and from the Ottawa connective as shown by McLaughlin (14). It is possible that plants from the Mississippi basin have been carried upstream by marginal eddy currents, which may carry drift for considerable distances. Also, the flat sandy bottoms which once carried glacial streams, such as the Mississippi, would have been favorable to the development of shifting beds, sloughs and marginal lakes where plants could establish themselves on the borders. The recession of the last ice advance left the Great Lakes region open to occupancy by vegetation. At that time the sand barrens, swales and lagoons resulting from glaciation were far more extensive than at present. It is reasonable to imagine that the shores of the glacial lakes giving rise to the present Lake Erie and Lake Michigan were a series of lagoons, ridges, strands and low dunes harboring the newly migrated coastal plain and strand types. No doubt a connective formerly existed across the Grand River valley of southern Michigan. Glacial Lake Warren in the Erie basin extended eastward into the Finger Lakes district of New York. When the Grand River connective ceased to function, Glacial Lake Lundy in the Erie basin found an outlet eastward past the ice margin down the Mohawk and Hudson River valleys. A connective between the part of Glacial Lake Algonquin which lay in the Lake Huron basin and Champlain Sea in the St. Lawrence-Ottawa valleys was finally opened by the continued reces-

TABLE III

RELIC, ENDEMIC, DISJUNCT AND COASTAL PLAIN SPECIES OF SHRUBS IN INDIANA

NAME OF SPECIES	Relic	Endemic	Disjunct	Coastal Plain	GENERAL DIRECTION OF MIGRATION					
					N	NE	NW	S	SE	E
Alnus rugosa				x		x			x	x
Andromeda glaucophylla	x				x	x	x			
Arctostaphylos uva-ursi var. coactilis	x				x	x	x			
Betula pumila	x				x	x				
Chamædaphne calyculata	x				x	x	x			
Cornus rugosa	x				x	x				x
Epigæa repens	x				x	x				
Hudsonia tomentosa var. intermedia	x			x		x				x
Hypericum kalmianum	x					x				
Juniperus communis depressa	x				x	x	x			
Myrica asplenifolia				x		x				x
Prunus pumila				x		x				x
Rhus toxicodendron				x		x		x	x	x
R. typhina				x		x		x	x	x
Salix adenophylla	x					x				
S. bebbiana				x		x				x
S. discolor				x		x				x
S. humilis				x		x		x	x	
S. petiolaris				x		x				x
Shepherdia canadensis	x				x	x	x			
Styrax americana			x	x				x	x	
Taxus canadensis	x				x	x	x			
Vaccinium macrocarpon	x			x	x	x			x	x
V. pennsylvanicum				x		x				x
Viburnum pubescens var. deamii		x								
V. pubescens var. indianense		x								
Total (26)	13	2	1	13	10	23	6	4	6	12

sion of the ice sheet to the north. Apparently, the pathway for the inland migration of the coastal plain flora was open sooner in the Hudson-Mohawk valley, since some plants indicate that they had followed the retreating ice front northward and later migrated up the Ottawa connective. It is altogether possible then that a species may be a glacial relic and a coastal plain species. While most coastal plain types are gradually dying out before the advance of the more aggressive floras, some species have spread to a greater or less extent in recent times wherever conditions favorable for their growth are found.

Table III lists species of shrubs which found a suitable environment during the former extensive migrations of plants and have remained in our flora as relic, endemic, disjunct and coastal plain species. While endemics also may be relics and disjuncts may be coastal plain species, they are listed in different columns. The general direction from which these species may have migrated into the state is given also. No claim is made that this list is exhaustive. (3, 5, 6, 10, 11, 14, 16, 25, 26, 27.)

PHYSIOGRAPHIC AREAS

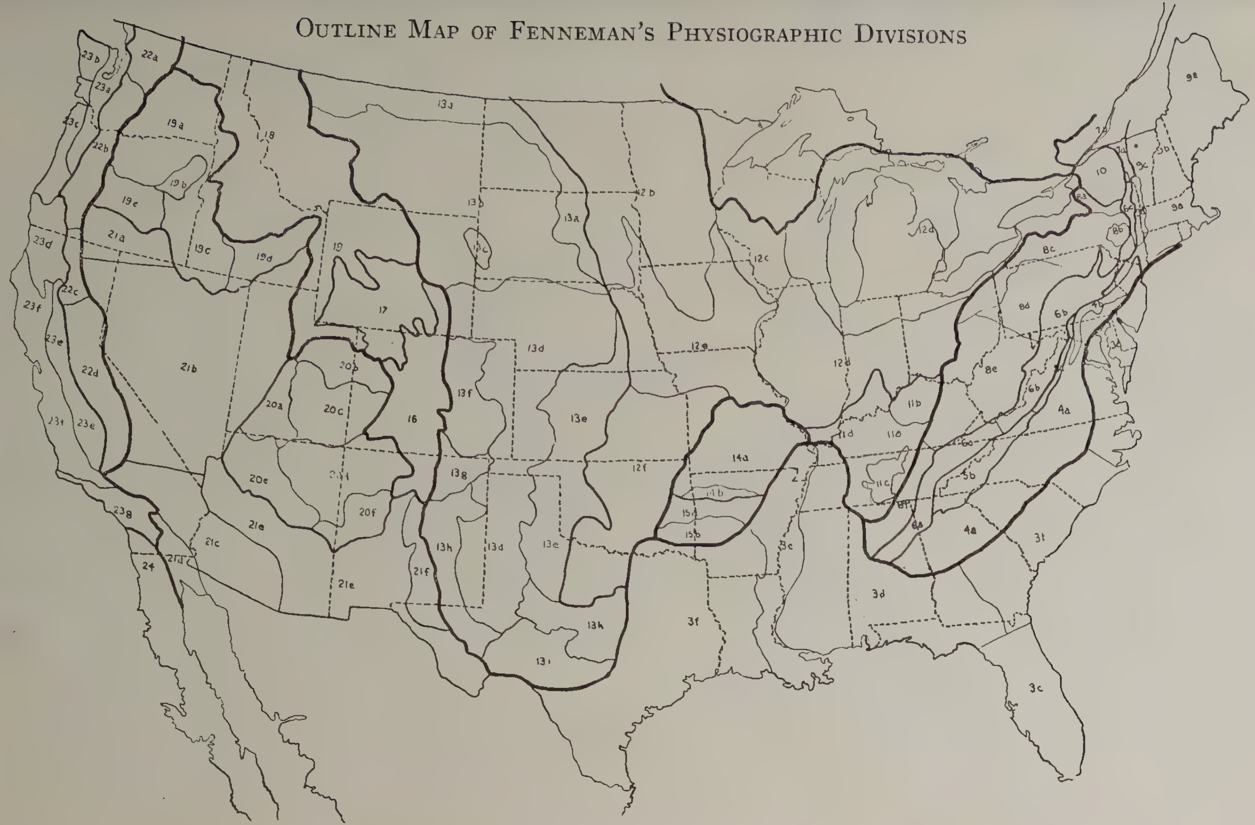
Since physiographic factors of habitat practically define the botanical areas within Indiana, a comparison of the shrubs in their wider distribution according to their physiographic location throughout the United States and parts of Canada seemed expedient. The topographically and edaphically determined habitats in the state have arisen during the course of physiographic development and have more or less definite relations to the larger physiographic features of the region. So natural areas were chosen rather than political divisions by states, because within an agreeable habitat a species may migrate freely regardless of specified state lines (15).

Fenneman (9) has divided the United States into eight strongly characterized parts called major divisions. The divisions are divided into units called provinces, units of the next smaller order being designated as sections. The major divisions are correlated with the great constructional events of geologic history. All orders of divisions rest ultimately on existing differences in topography and elevation, the differences considered being those which pertain to physiographic types and not merely to superficial appearance. This work of Fenneman, therefore, offers the best natural differentiation of areas for showing the physiographic distribution of the shrubs of Indiana. Map II shows these divisions in outline. For an enumeration of these divisions the paper by Lindsey (12) should be consulted.

PHYSIOGRAPHIC DISTRIBUTION

Of the 212 species of shrubs given by Deam (Table I), twenty-six are disregarded concerning their wider distribution, due to the fact that sufficient information could not be obtained which would fix their ranges to any reliable extent. The ignored species are as follows: *Amelanchier humilis* x *Amelanchier laevis, XBetula purpusii, Crataegus barrettiana,* MAP 2

Outline Map of Fenneman's Physiographic Divisions



C. conjuncta, C. gracilis, C. gracillipes, C. ignea, C. meticulosa, C. palustris, C. parviflora, C. rutila, C. sejuncta, C. trahax, Lonicera dioica var. *glaucescens* forma *dasygna, Prunus virginiana* var. *demissa, Ptelia trifoliata* var. *deamiana, P. trifoliata* forma *mucronata, Rosa blanda* var. *hispida, R. carolina* var. *sabulosa, R. deamii, R. relicta, Sambucus canadensis* forma *atroflavula, Vaccinium corymbosum* var. *atrocarpum, V. vacillans* var. *crinitum, Viburnum acerifolium* forma *ovatum, Vitis vulpina* var. *syrticola.*

For the 186 shrubs which remain, ranges were determined after Deam (8), Rosendahl and Butters (21), Britton and Brown (1), Small (24), Robinson and Fernald (20), Coulter and Nelson (2), a few species of Rosa by Rydberg (22) and some species of Cratægus by Sargent (23). If a check list of all shrubs appearing in each state in the United States could be obtained, no doubt the range of many shrubs would be extended. A large table was prepared which contained all the physiographic areas of Fenneman. After checking the entire range of each shrub, the number of species appearing in each province or section was totalled and its percentage of the entire number of 186 shrubs found. Percentage classes were found in order to compare the density of species of the different provinces and sections in this manner: Under per cent class No. 1 is listed the section containing between 91-100 per cent of the 186 shrubs; class No. 2, the provinces and sections containing between 81-90 per cent, and other classes in descending order of 10 per cent intervals, making ten classes in all. Table IV gives the percentage classes which show the result of this tabulation.

Map 3 shows by shadings the variations in density of the Indiana shrubs over their entire range. The shadings are representative and not absolute, because provinces and sections are not sharply divided and the ranges of all species are not yet accurately drawn. The map reveals the general distribution within the United States of all the Indiana shrubs.

The section of heaviest density with respect to number of species in Indiana falls in the Lake region (Fenneman's division 12a). Lindsey (12) found that the section of heaviest density for the trees included the following: Tipton Till Plain, Prairie, Lower Wabash Valley and the Flats (Fenneman's division 12d). The greater density of the shrubs in the Lake area is undoubtedly due to the presence of so many bogs and lakes which have not yet passed the shrub stage on their way toward the mesophytic forest climax. Further, it has been stated that many of the shrubs

TABLE IV

PERCENTAGE CLASSES FOR SHOWING THE VARIATIONS IN DENSITY OF THE DIFFERENT PHYSIOGRAPHIC DIVISIONS

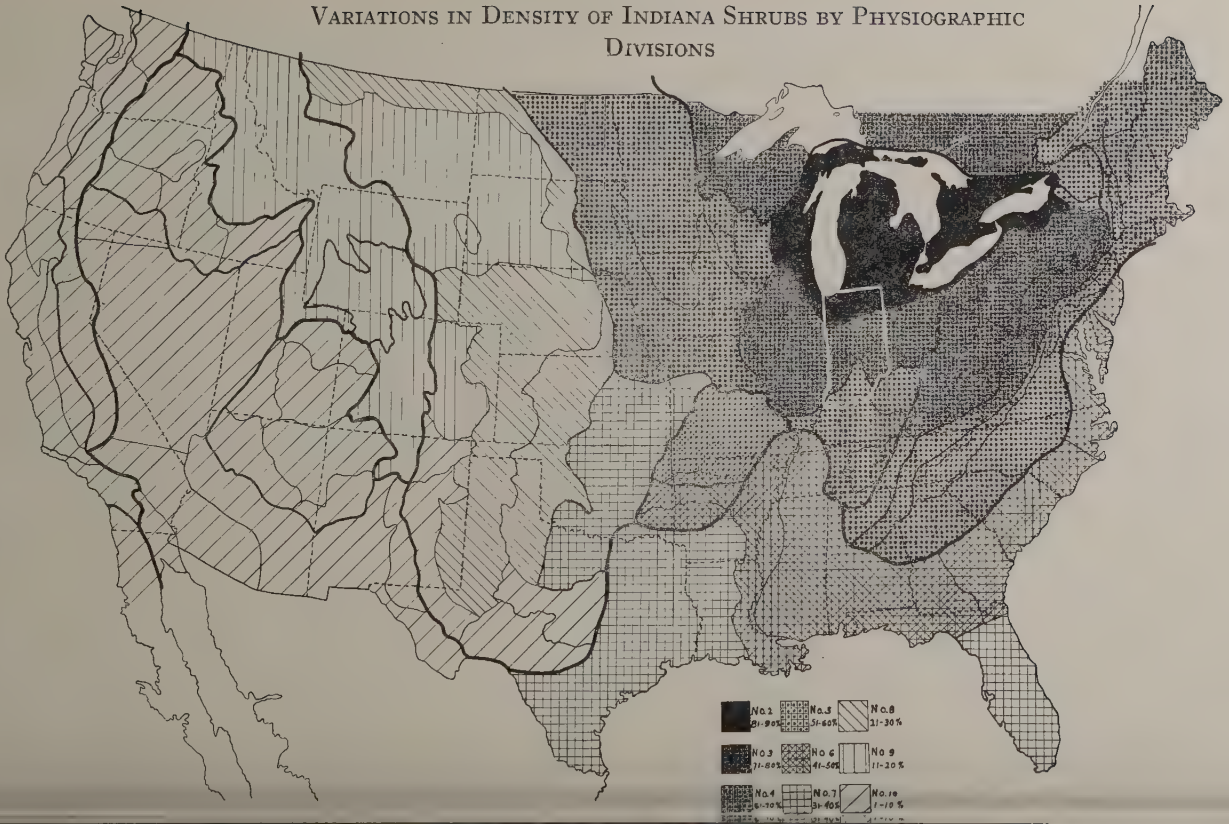
PER CENT CLASS	NO.	PHYSIOGRAPHIC AREAS IN PERCENTAGE CLASS
91-100	1	None
81- 90	2	12a
71- 80	3	1; 6b; 8b; 8c, 8d, 8e; 12d
61- 70	4	4a, 4b; 5a, 5b; 6a, 6c; 7a, 7b; 8a, 8f; 9a, 9b, 9c, 9d; 10; 11a, 11b, 11c, 11d; 12b, 12c, 12e
51- 60	5	14a
41- 50	6	3a, 3b, 3d, 3e; 14b; 15a, 15b
31- 40	7	3c, 3f; 12f
21- 30	8	13a, 13d, 13e
11- 20	9	13b, 13c, 13f; 16; 17; 18
1- 10	10	13g, 13h, 13i, 13k; 19a, 19b, 19c, 19d, 19e; 20a, 20b, 20c, 20d, 20e, 20f; 21a, 21b, 21c, 21d, 21e, 21f; 22a, 22b, 22c, 22d; 23a, 23b, 23c, 23d, 23e, 23f, 23g; 24

characteristic of other areas also find suitable habitats in the Lake region, while in addition many typical bog and lake shrubs occur in the Lake era and not elsewhere. The real significance of the difference between location of areas of greatest density of trees on the one hand and shrubs on the other is the fact that much of the state outside of the Lake region has passed the shrub stage of succession into the tree stage toward the vegetational climax.

The area of heaviest density is surrounded by two density classes, numbers 3 and 4 of the descending order. Density class 3 surrounds the section of heaviest density except for parts at the east and west where density class 4 is contiguous. This means that only two lanes of different numerical value radiate from a common center. There is a somewhat definite correlation between a density class and its distance from the region of heaviest density, the density decreasing gradually with the distance to the south, southeast, southwest, and the distant west; very gradually to the north, northeast and northwest. For example, class number 6 is on the whole farther from the region of heaviest density than class number 5. All of the density classes present an irregular arrangement because of the abrupt ending of ranges and the irregular outlines of the sections and provinces. Only three classes, 5, 9 and 10, are central-

MAP 3

VARIATIONS IN DENSITY OF INDIANA SHRUBS BY PHYSIOGRAPHIC DIVISIONS



ized and have a general direction of extension. Class 5, occupying the fifth heaviest density area, is southwestern; class 9 is middle western, and class 10 is far western. The remaining classes are not confined to a single direction. The shrubs of Indiana have their ranges most generally in the eastern half of the United States, but more shrubs than trees of Indiana have ranges in the western half of the United States, since the prairies do not present such a barrier to the shrubs as to the trees. Indeed, some of the shrubs serve as a connecting link between the deciduous forests of the east and the prairies of the west.

The distribution of Indiana shrubs, shown graphically on Map 3, is in accordance with physiographic affinity, since the physiographic range of a species indicates in a general way the type of minor physiographic or botanical area it occupies in Indiana. For example, the shrubs of the Lake region occupy similar physiographic regions in their wider distribution. Those of the Lower Wabash Valley occupy similar habitats to those of this area in their general distribution. The "all over" species in Indiana show no marked preference for certain physiographic areas in their wider distribution.

SUMMARY AND CONCLUSIONS

1. Twenty-three per cent of all Indiana shrubs are found in all the botanical areas. The percentage of the different botanical areas appear in this descending order: Lake region, Tipton Till Plain, the Knobs, the Flats, the Lower Wabash Valley and the Prairie regions.

2. The Lake region is especially distinctive in its possession of exclusives, having almost twice as many exclusives as all other areas combined.

3. Each species limited to one botanical area in Indiana is on the limit of its range and is extraneous in its distribution.

4. The extraneous species lie in four general directions from Indiana, and in each case the direction is usually in direct relation to the physiographic character of the botanical area in which the species is found, *viz.*, Lake region exclusives to the northeast; Knobs exclusives to the southeast; Lower Wabash Valley exclusives to the south; and Prairie exclusives to the west. These species, however, may have extensions in one or more adjoining directions.

5. Shrubs found in all areas of the state and most of those that are

characteristic of a particular botanical area are intraneous species and are well within their ranges in Indiana.

6. Fifty-six per cent of all Indiana shrubs have range limits in Indiana. Of these, 41 per cent are exclusives in one or other of the botanical areas and the remainder range in two or more areas, but not in all.

7. A number of relic, endemic and disjunct species are found among the shrubs of Indiana. These were left in our area by the advance and retreat of the glaciers.

8. The strongest affinity of Indiana shrubs for physiographic provinces, in part, or totally outside of Indiana, is to the north, northeast, and northwest. The weakest affinity is to the west, beginning with the Great Plains and continuing westward.

9. The physiographic provinces occupied by a species indicates in a general way the type of minor physiographic (botanical area) it occupies in Indiana.

The writer wishes to express sincere appreciation to Dr. Ray C. Friesner for suggesting this study and for valuable help and encouragement received from him as the study progressed; to Mr. Charles C. Deam for his interest and kindness in sending his unpublished manuscript of the second edition of Shrubs of Indiana at a time when this work could not have progressed except for this help.

LITERATURE CITED

1. Britton, N. L., and Addison Brown. Illustrated flora of northern United States and Canada. 2 ed. Charles Scribner's Sons. 1913.
2. Coulter, John M., and Aven Nelson. New manual of Rocky Mountain botany. American Book Co. 1909.
3. Coulter, John M., and Harvey Thompson. The origin of Indiana flora. Indiana Geol. and Nat. Hist. Report 15:253-282. 1885-1886.
4. Cowles, Henry C. The content and scope of physiographic ecology. Bot. Gaz. 31:73-108; 145-182. 1901.
5. —— The succession point of view in floristics. Proc. Int. Cong. Plt. Sci. Ithaca 1:687-691. 1926.
6. Deam, Charles C. Flora of Indiana: on the distribution of the ferns, fern allies and flowering plants. Indiana Acad. Sci. Proc. 34:39-52. 1924.
7. —— Trees of Indiana. 4 ed. Pp. 18; 299-300. Indiana Dept. Conservation. 1931.
8. —— Shrubs of Indiana. 2 ed. Indiana Dept. of Conservation. 1932.
9. Fenneman, Nevin M. Physiographic divisions of the United States. Ann. Assoc. of Amer. Geog. 6:19-98. 1916.
10. Fernald, M. L. Specific segregations and identities in some floras of eastern North America and the Old World. Rhodora 33:25-63. 1931.
11. Gleason, Henry A. The vegetational history of the Middle West. Ann. Assoc. Amer. Geog. 12:39-85. 1923.
12. Lindsey, Alva J. The trees of Indiana in their local and general distribution according to physiographic divisions. Butler Univ. Bot. Stud. 2(9):93-124. 1932.
13. Lyon, Marcus W., Jr. List of flowering plants and ferns in the Dunes state park and vicinity, Porter county, Indiana. Amer. Midland Nat. 10(8-9):245-295. 1927.
14. McLaughlin, W. T. Atlantic coastal plain plants in the sand barrens of northwestern Wisconsin. Ecol. Monog. 2:336-380. 1932.
15. Nichols, George E. A working basis for the ecological classification of plant communities. Ecol. 4:11-23; 154-177. 1923.
16. Peattie, Donald C. The Atlantic coastal plain element in the flora of the Great Lakes. Rhodora 24:57-70; 80-88. 1922.
17. —— Flora of the Indiana dunes. Field Museum. 1930.
18. Pepoon, H. S. An annotated flora of the Chicago region. Chicago Acad. Sci. Chicago. 1927.
19. Price, Gladys, and Winona H. Welch. Enumeration of the vascular flora of a limestone area of the Bloomington quadrangle, Monroe county, Indiana. Indiana Acad. Sci. Proc. 39:131. 1929.
20. Robinson, B. L., and M. L. Fernald. Gray's new manual of botany. 7 ed. American Book Co. 1908.
21. Rosendahl, C. O., and F. K. Butters. Trees and shrubs of Minnesota. University of Minnesota Press. 1928.
22. Rydberg, Axel. Roseaceæ. North Am. Flora. 22(5):443. 1913; 22(6):499; 500; 509. 1918.

23. Sargent, Charles S. Manual of trees of North America. 2 ed. Pp. 406-407; 409; 490-491. Houghton Mifflin Co. 1922.

24. Small, John K. Flora of the southeastern United States. 2 ed. J. K. Small, New York. 1913.

25. Thompson, Maurice. Geographical botany. Indiana Geol. and Nat. Hist. Report 15:242-252. 1885-1886.

26. Warming, Eugene. Œcology of plants, pp. 11-80; 368-373. Oxford Univ. Press. 1925.

27. Welch, Winona H. A contribution to the phytoecology of southern Indiana with special reference to certain Ericaceæ. Indiana Acad. Sci. Proc. 38:65-83. 1928.

28. —— Forest and prairie, Benton county, Indiana. Indiana Acad. Sci. Proc. 39:67-72. 1929.

THE EFFECT OF INTERRUPTED TRANSLOCATION UPON LOSS OF CHLOROPHYLL IN LEAVES DURING AUTUMN COLORATION[1]

By AGATHA GRIFFIN

Palladin (7) makes the unrestricted statement in his Plant Physiology: "If an incision is made in a leaf in the autumn while it is still green, so that the chlorophyll decomposition products are prevented from diffusing away, the part of the leaf above the cut remains green while the other parts turn yellow." In support of this statement he cites work by Stahl (8) and reproduces an illustration of the Ginkgo leaf from this author.

In accord with the long existing conception that valuable substances are translocated out of leaves, before abscission, to permanent parts of the plant in order to preserve the synthates for the plant, Stahl believed that a substance as valuable to the plant as the green chlorophyll pigment would not merely be destroyed by light and absorbed in situ (*i. e.*, in the leaf cells). In his opinion, the results of his experiment offered significant evidence of the translocation of decomposition products of chlorophyll from dying leaves.

Using green leaves of *Æsculus rubicunda* and of *Ginkgo biloba* which were about to discolor, Stahl made incisions which severed either the lateral veins or the midrib of the leaves. In every case, discoloration was extremely retarded above the cut; in the Ginkgo leaves the portions above the cut remained green after the rest of the leaf had become entirely yellow. In other experiments, portions of leaves remained green when cut off from translocation channels by creasing the leaf, by entirely severing the top of the leaf or a disc from the anatomical unit, or by removing an entire leaf from the stem (Table I). Since moisture and all other environmental conditions were identical, Stahl concluded such behavior indicated that interrupted translocation caused the retention of green color in portions so controlled. His conclusion was based on positive results from eleven species (Table I). Two additional species, *Polygonatum multiflorum* and *Funkia sieboldiana*, showed negative results, but he felt these might be correlated with his theory upon further investigation. However, he severed the veins in only two of the eleven species; and Palladin used this part of Stahl's experiment, involving only two species, as the basis for his statement that during autumn coloration the part of the leaf above an incision remains green while the part below turns yellow.

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[1] A portion of a thesis submitted to the committee on graduation honors in partial fulfillment of the requirements for the honor *Magna cum Laude*, Butler University, June, 1934.

In the present experiment, eighteen species were examined to observe the effect of an incision through the vein upon loss of chlorophyll above and below the incision during autumn coloration.

TABLE I

INFLUENCE OF INTERRUPTED TRANSLOCATION UPON LOSS OF CHLOROPHYLL IN LEAVES. TABULATION OF RESULTS OBTAINED BY STAHL (8)

SPECIES	TECHNIQUE	RESULT Interrupted Portion	Normal Portion
Philadelphus grandiflorus	Severed leaf	Loss of green retarded	Yellow
Robinia viscosa	Severed leaf	Loss of green entirely prevented	Yellow
Philadelphus grandiflorus	Disc removed from leaf	Entirely prevented	Yellow
Ulmus montana	Disc removed from leaf	Entirely prevented	Yellow
Betula verrucosa	Disc removed from leaf	Entirely prevented	Yellow
Robinia pseudoacacia	Half of leaf completely severed	Entirely prevented	Yellow
Æsculus rubicunda	Bending leaf blade crushed tissue	Retarded	Yellow
Ginkgo biloba	Same	Retarded	Yellow
Robinia viscosa	Same	Retarded	Yellow
Acer platanoides	Same	Retarded	Yellow
A species of Quercus	Same	Retarded	Yellow
Æsculus rubicunda	Incision through vein	Retarded	Yellow
Ginkgo biloba	Incision through vein	Retarded	Yellow
Monocotyledons			
Polygonatum multiflorum	Incisions and discs	Hastened loss of green	Green
Funkia sieboldiana	Incisions and discs	Hastened loss of green	Green
Agapanthus umbellatus	Discs	Retarded	Yellow
Kampheria pandurata	Discs	Retarded	Yellow
Chlorophytum orchidastrum	Discs	Retarded	Yellow

PROCEDURE

On October 3, 1933, incisions were made through the veins of unshaded green leaves still growing on the tree. Sets of ten leaves were cut on opposite sides of each tree to compare results under both morning and afternoon sunlight. (See Table II.) Each group of ten leaves included several types of incisions: (1) through the midrib only, (2) through the midrib and another through a lateral vein, (3) through a single lateral vein, and (4) through several adjacent lateral veins. Observations were recorded at three-day intervals, either until leaves showing definite results were gathered or until leaves showing no results had fallen from the tree.

On October 17, incisions were made in new sets of leaves of *Liriodendron tulipifera, Morus tatarica* and *Ginkgo biloba,* species which had, so far, shown no definite results. To ascertain whether or not late cutting was a determining factor in the results obtained, duplicate sets of *Acer saccharum* and *A. rubrum* were cut to compare with the sets cut early in October. On October 24, *Quercus macrocarpa, Liquidambar styraciflua, Prunus serotina, Berberis thunbergii,* and the grass, *Setaria lutescens* were added to the species previously included in the experiment. A new set was cut for *Q. imbricaria,* also.

The leaves observed were mounted and deposited in the Herbarium of Butler University and drawings were made from the original material.

RESULTS

The results obtained from the present experiment were not so uniform as those obtained by Stahl. The reaction, with few exceptions, was uniform for the leaves of any one species, irrespective of the type of incision, in every case becoming evident in the region controlled by the cut. However, the different species examined showed three distinct types of results. Nine species lost the green color above the incision while the remainder of the leaf was still green; six species showed no difference in the region above and below an incision, both areas either turning yellow or both remaining green; only three species remained green above the cut while the lower section turned yellow (thus agreeing with Palladin's statement). Results are shown in Table II.

Galls on the veins of leaves of *Quercus alba* (Figure 4) produced effects similar to those resulting from incisions, *i. e.*, in every instance the region above the gall lost chlorophyll first. Microtome sections through such gall-infested areas showed a definite modification of the vascular tissues, thus correlating the ultimate effect on translocation somewhat with that of an incision.

Leaves turning red or orange only above the incision (while the lower part remained green) were classed with those losing chlorophyll above the cut on the assumption that anthocyanin does not become evident until chlorophyll disappears (6), and especially since not a trace of green was evident in the red areas. Identical results were obtained in leaves exposed to morning and afternoon sunlight, indicating that the intensity, kind of light and length of exposure were seemingly not directly responsible for the results obtained.

Prunus serotina failed to show the reaction exhibited by most species, but it was listed with those losing chlorophyll above the cut because most leaves showed such behavior.

Leaves of *Acer saccharum,* cut October 17, failed to produce the bright orange-red color exhibited above the incision by the leaves cut October 3. This second set showed no change for a week; three days later the majority of leaves were entirely yellow both above and below the cut, while three leaves remained a light yellow-green in the region above the incision. *Quercus imbricaria* and *Acer rubrum* both exhibited identical reactions in sets cut October 2, October 24 and October 17, respectively.

Regions above incisions in the leaves of *Ginkgo biloba* immediately withered, changing to the characteristic brown of dead tissue and making observations on the loss of green in normal tissue impossible. The same result was obtained in a second set. However, about a month after removing the leaves from the tree, the dead tissue appeared green again.

An experiment performed with eosin solution to determine the path of water translocation showed no eosin present above the incision in the parallel-veined species examined (*Miscanthus sinensis* and a species of Lilium) while in net-veined species eosin was translocated around the cut through secondary veins. Prevention of water translocation to the area segregated by an incision in parallel-veined leaves suggests that the retention of chlorophyll above the incision in the Ginkgo leaves of Stahl's experiment was probably due to the death of the tissues and not to the accumulation of decomposition products. Conditions in the Ginkgo leaves of the present experiment were certainly not comparable to those in other species; and it is difficult to see how Stahl could have preserved normal tissue above an incision in the parallel-veined leaf of Ginkgo.

TABLE II

Loss of Chlorophyll in Leaves with Severed Veins

Leaves Losing Green Color Above Incision (Yellow or Red Above Cut)	Leaves Remaining Green Above Incision	Leaves Not Influenced by Cut. (Identical Above and Below Incision)	
Acer saccharum (Fig. 2)	Ginkgo biloba	Acer platanoides	Green
A. rubrum (Fig. 1)	Liquidambar styraciflua (Fig. 3)	Cornus asperifolia	Green
Berberis thunbergii	Quercus macrocarpa (Fig. 7)	Fagus grandifolia	Yellow
Nyssa sylvatica		Liriodendron tulipifera	Yellow
Prunus serotina		Morus tatarica	Green
Quercus alba (Fig. 4)		Platanus occidentalis	Green
Quercus imbricaria (Figs. 5, 6)			
Rhus glabra			
Setaria lutescens			

DISCUSSION

Stahl's inconsistent use of the terms "chlorophyll," "green pigment" and "decomposition products" as interchangeable terms, leaves the reader confused as to his actual conception of the disappearance of chlorophyll. Evidently he believed that chlorophyll decomposition products are translocated out of the dying leaf; but the accumulation of these products retards chlorophyll decomposition.

Recent work throws some light on facts underlying the theory of translocation of valuable substances to perennating parts before leaf-fall with which Stahl was attempting to correlate the disappearance of chlorophyll in autumn. Rippel, according to Denny (2), reported a loss of 52 to 81 per cent of nitrogen in the leaves of thirty-three species. However, Denny (2) observed only very small changes in Syringa and Viburnum, a consistent decrease of 35 to 40 per cent of nitrogen in Viburnum being the only positive result he obtained; the nitrogen content of Syringa and the sugar content of both remained nearly constant. Combes (1) was the first to prove by measurement of nitrogen in stems and roots as well as in leaves that the amount increases in the stem and roots as the amount in the leaf decreases during yellowing. Significant results, obtained by comparison of absolute amounts rather than as percentage of dry weight, showed that the leaves of sixteen two-year-old oak plants lost 33.73 milligrams of nitrogen during yellowing, while the stems gained 3.94 milligrams and the roots gained 22.26 milligrams during the same period.

At the time of publication of Stahl's paper, Wehmer, according to Stahl (8), was vigorously opposing the theory that substances necessary in plant metabolism were translocated to perennating tissues. He not only pointed out that the reduction of phosphoric acid and potash might be due to leaching in dying leaves, but declared that translocation was impossible, since reduction of valuable substances occurred after formation of the abscission layer which, he considered, inhibited further translocation.

Tison, according to Stahl (8), had found that the parenchyma tissues of the vascular bundles examined were almost devoid of corky layers so long as the leaf had not fallen; Kienitz-Gerloff, according to Stahl (8), supported the possibility of translocation with evidence that the sieve tubes of veins in discoloring leaves were still filled with protoplasm. Holman and Robbins (3) state that when the abscission layer is formed, the conducting elements of vascular bundles generally remain unaffected. However, Lee's (5) detailed microscopic observation of the formation of the abscission layer in nine species strongly supports Wehmer's contention. At the first appearance of the abscission layer, tyloses and gummy lignins formed in the vascular bundles of all species. Lee definitely states that in *Castanea sativa,* Salix, *Prunus cerasus* and *Rhus typhina* the conducting elements were obstructed, stopping the flow of nutrient solutions from the stem.

When Kolkwitz (4) performed his experiments, based on Stahl's work (8), he found so many exceptions to a behavior indicative of chlorophyll translocation to perennating tissue that he concluded "an assumption of chlorophyll pigment disposition for teleological reasons is impossible." Leaves of *Syringa vulgaris,* Ligustrum, and occasionally *Fraxinus excelsior,* abscised while still green, and in the case of *Syringa vulgaris,* while still capable of photosynthetic activity, showing that translocation of decomposition products had not occurred. Leaves of *Brassica oleracea acephala,* deficient in nutrients and removed from the plant, yellowed as rapidly as attached leaves, showing that rapid discoloration may occur when decomposition products are not removed. The varied results of the present experiment indicate that the accumulation of decomposition products does not always inhibit chlorophyll decomposition.

However, the question then arises whether an incision through the vein always prevents translocation of these products, as Palladin claims. Stahl reported only retarded loss of green above the incisions in *Æsculus rubicunda* and *Ginkgo biloba;* he did not claim that an incision prevents translocation entirely. The present eosin experiment showed that in net-veined leaves the water is translocated around the cut by smaller veins to tissue above the incision. Translocation of waste products by the same path probably occurs. Had all net-veined leaves failed to remain green above the incision, while parallel-veined leaves, in which an incision means absolute interruption of translocation, remained green, the failure to confirm Stahl's results might be explained by the failure of waste products to accumulate. Unlike the entirely severed discs, tips of leaves and entire severed leaves, incisions through the veins of net-veined leaves evidently do not result in absolute interruption of translocation.

If all leaves had remained green above the incision, as Palladin's statement leads one to expect, one would be justified to assume that accumulation of waste products is the factor which controls the decomposition of chlorophyll. However, results of this experiment prove that any general statement as to the decomposition of chlorophyll when waste products are not removed is not justified; but they rather indicate that some other modifying factor, dependent on the species, influences chlorophyll decomposition.

SUMMARY AND CONCLUSIONS

1. The leaves of eighteen species of plants were examined to determine the effect of severed veins upon autumnal loss of chlorophyll.

2. Disappearance of chlorophyll in leaf areas above interrupted translocation varied with different species.

3. Four patterns of discoloration in leaves were obtained when incisions were made through the veins shortly before autumnal coloration. Nine species lost the green color above the incision first; two species discolored simultaneously above and below the cut; four species remained green both above and below the incision; only three species remained green above the cut and discolored below.

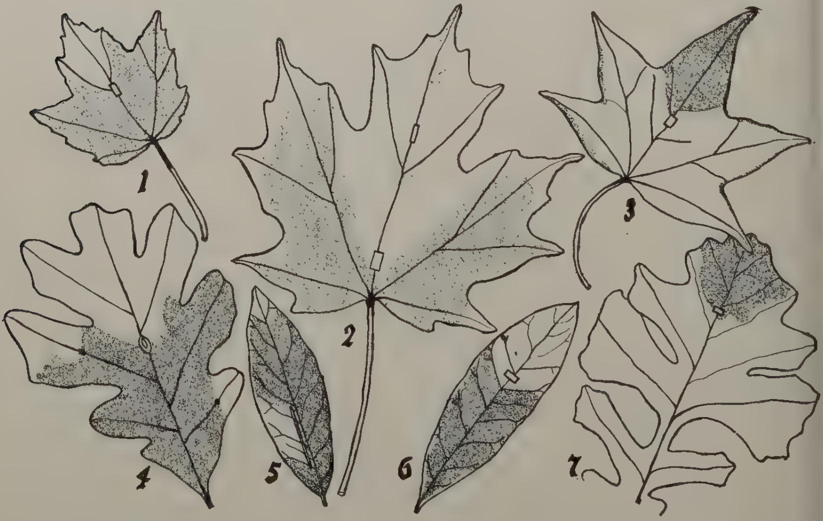
4. Translocation of eosin in net-veined species through secondary veins to all veins above a cut in a leaf suggests that probably an incision through the vein does not prevent the removal of decomposition products entirely from areas of interrupted translocation in net-veined leaves.

5. The varied results of this experiment show plainly that the pre-

vention or retardation of the removal of decomposition products of chlorophyll does not operate (if at all) as a universal law, governing all species, in preventing the breaking down of chlorophyll by inhibition of some chemical process, as assumed by Stahl and accepted by Palladin.

6. *Ginkgo biloba* is not well adapted to the type of experiment used in this observation because areas above severed veins die too readily and thus obscure results.

Appreciation is here extended to Dr. John E. Potzger, of the Butler University Department of Botany, for suggesting and supervising this study, as well as for translations of the German articles considered in this thesis.



Explanation of Figures—Effect of severed veins on the disappearance of chlorophyll from leaves: Dark areas indicate presence of chlorophyll, light areas its absence. Rectangles indicate cut through veins. (1) *Acer rubrum;* (2) *A. saccharum;* (3) *Liquidambar styraciflua;* (4) *Quercus alba*, discoloration above gall injury; (5, 6) *Q. imbricaria;* (7) *Q. macrocarpa.*

BIBLIOGRAPHY

1. Combes, Raoul. Emigration des substances azotées des feuilles vers tiges et les racines des arbres au cours du jaunissement automnal. Biol. Abs. 1: Entries 6521-23. 1926-27.
2. Denny, F. E. Changes in leaves during the period preceding frost. Contr Boyce Thompson Inst. Plt. Res. 5:297-312. 1933.
3. Holman, R. M., and W. W. Robbins. Textbook of general botany. London: John Wiley & Sons. 1928.
4. Kolkwitz, R. Uber das Schicksal des Chlorophylls bei der herbstlichen Laubverfärbung. Ber. Deut. Bot. Ges. 37:2-5. 1919.
5. Lee, E. The morphology of leaf fall. Ann. Bot. 25:51-106. 1919.
6. Onslow, M. W. Anthocyanin pigments of plants, p. 82. New York: Macmillan Co. 1927.
7. Palladin, Vladmir I. Plant physiology, p. 16. Philadelphia: P. Blakiston's Son & Co. 1926.
8. Stahl, Ernst. Zur Biologie des Chlorophylls; Laubfarbe und Himmelslicht, Vergilbung und Etiolement. Jena. 1909.

SOME NOTES ON ANTHOCYANIN FORMATION IN LEAVES WITH CUT VEINS[1]

By Agatha Griffin

The observations on loss of chlorophyll in parts of leaves above cut veins reported in the preceding paper brought out some rather striking features concerning anthocyanin formation in such segregated areas, which seemed worthy of special consideration and are here presented.

Anthocyanin seemed to form in abundance in areas above cut veins in many species observed, although, according to the United States Weather Bureau (1), no frost occurred during that time. Freezing temperature was approached but once, *viz.*, on October 25. Such observations are in accord with the opinion of Hass and Hill (3), that anthocyanin forms at low temperature, but does not require frost for its development.

In order to determine what effect incisions through veins had upon sugar accumulation, one-inch squares were cut from areas above and below severed veins, ground in a mortar and tested with Fehling's solution. While such a test is not quantitative in the strict sense of the word, varying amounts of red precipitate gave some quantitative conception. Amount of cuprous oxide produced forms the basis of all subsequent comparisons of amount of sugar present. Unfortunately, the tests were only for reducing sugars and so no comparisons can be made on total sugars present in the leaves. In *Acer saccharum, Quercus alba* and *Rhus glabra,* much more sugar was present above the incision where anthocyanin was very pronounced than in the green area below the cut. This was also true of *Quercus imbricaria* where the leaf had turned yellow above the cut, but remained green below. However, a second set of leaves, cut on October 24, turned a decided red above the incisions.

In *Fagus grandifolia,* where the whole leaf turned yellow, and in *Morus tatarica,* where the leaf remained uniformly green all over, more sugar was present above the cut than below. In *Liriodendron Tulipifera* and *Platanus occidentalis* the leaves discolored uniformly above and below the incision and no marked difference in sugar accumulation was noted in areas of interrupted translocation. None of these four species is known to develop anthocyanin. The formation of the pigment is thus not merely dependent on the presence of abundant sugar supply, but other factors must evidently enter in.

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[1] A portion of a thesis submitted in partial fulfillment of the requirements for the graduation honor *Magna cum Laude,* Butler University, June, 1934.

The leaves of *Quercus alba* injured by galls also produced anthocyanin above the injury while the portion of the leaf below the injury was still green. Most sugar was present in the portion of the leaf where anthocyanin had formed. The accumulation apparently was due to the modifications of the vascular tissues in the veins, thus retarding translocation. Onslow (4) believes that the formation of pigment in insect-injured leaves is directly associated with an accumulation of sugar, due to an interference in the translocation channels. Thus the present observations harmonize with such an interpretation.

The first set of leaves of *Acer saccharum* with cut veins were readily located on the tree after discoloration of the green had occurred because the portions above the incisions were a conspicuous orange-red, while normal leaves and the parts below the incision merely turned yellow. Similar results were obtained in *Acer rubrum*. Not every leaf cut on October 3 developed anthocyanin above the incision; some merely turned yellow, but whenever anthocyanin formed, it was in areas controlled by an incision. All leaves of this species cut on October 17 produced anthocyanin above the incision. Leaves of this tree showed no anthocyanin formation besides this except in leaves where insect injury had interfered with the avenues of translocation, and there only above the injury.

In the species enumerated thus far, anthocyanin formation was limited to the area above the incision even after the leaf finally lost all chlorophyll. In the following species, anthocyanin formed first above the incision, but ultimately involved the whole leaf: *Nyssa sylvatica, Prunus serotina, Rhus glabra, Berberis Thunbergii* and *Quercus imbricaria*, cut on October 22.

All of these results seem to indicate that anthocyanin formation is hastened or facilitated by interrupted translocation, with accompanying greater sugar accumulation in species which normally might produce anthocyanin. They also support the evidence obtained by Overton, Gertz and Katic (2) that accumulation of sugar is a determining factor in the formation of anthocyanin in leaves.

BIBLIOGRAPHY

1. ARMINGTON, J. H. Climatological data. U. S. Dept. Agr. Weather Bureau, Indianapolis, Indiana, 38 (10):40. October, 1933.
2. SMITH, GILBERT M., J. B. OVERTON and E. M. GILBERT. Textbook of general botany. New York: Macmillan Co. 1928.
3. HAAS, PAUL, and T. G. HILL. Chemistry of plant products. London: Longmans, Green & Company. 1928.
4. ONSLOW, MURIEL WHELDALE. The anthocyanin pigment of plants. London: Cambridge University Press. 1925.

A NEW METHOD FOR SEPARATION OF FOSSIL POLLEN FROM PEAT

By Florence Geisler

Paleoecology, as any other type of research, has its encumbent difficulties. Chief among these is, no doubt, the fogging of truth by errors introduced by methods. One of these difficulties in fossil pollen study is the separation of the pollen grains without anatomical or numerical distortion from the debris of plant remains in which they lie embedded. Sears (6) says, "It is a safe rule to use the mildest treatment which will completely loosen all pollen from the floccules." This problem of technique is as old as the study of fossil pollen, but we recognize introduced errors more keenly as time goes on. Before presenting the new method for separation of peat, it seems well to outline briefly the procedure in the more common present methods and point out some of the errors they introduce into the observations.

OUTLINE OF SOME PRESENT METHODS

Sears (6) summarizes the most common method thus: "A piece of material not larger than 10 mm. in diameter is placed in a 10 per cent solution of KOH and boiled down." Glycerine is then mixed with the peat, some of which can then be transferred to a slide and mounted.

G. Erdtman and H. Erdtman (4) call the alkali method "a rather severe treatment," and claim a source of error is introduced by different intensities of boiling to which the samples may be subjected. These workers also present some figures showing that, "After a double boiling with alkali there is a decrease in the pine pollen frequency and an equally marked increase in birch pollen. The frequencies of the other pollen are not changed."

Potzger (5) objected to the use of potassium hydroxide for separation of peat because of the apparent error introduced by distortion of the pollen grains. In fact, most workers apologize more or less for the alkali method for separation of pollen in fossil peat because of its severity. G. Erdtman and H. Erdtman (4) recognize and admit this defect in the method and offer a new method in its place. This new method, however, seems even more severe than the old potassium hydroxide method, yet they recommend it especially for the treatment of peats having a low pollen content. They describe the process thus:

"Sphagnum peat was mixed with cold 10 per cent sodium hydroxide solution and stirred until a semiliquid mass was obtained. After a few hours it was pressed through a metal net (meshes 4 mm.) in order to remove coarse débris such as twigs, etc. After acidification with dilute hydrochloric acid (1:1) the peat was filtered with suction on a Buchner funnel and washed with water until the filtrate gave only a weak test for chlorine ions with silver nitrate. The peat was then spread on glass plates and dried at a temperature slightly above room temperature. The dried peat was carefully ground in a mortar and sifted (meshes 0.4 mm.). The peat thus obtained was used as standard peat in our experiments."

The lignin and humic acid components were next destroyed by oxidizing agents. "In a Petri dish, 0.2 g. standard peat were added to a mixture of 8 cc. glacial acetic acid and 4.5 cc. sodium chlorate solution (100 g. $NaClO_3$ and 200 cc. distilled water). One cc. sulphuric acid (80 per cent) was carefully added, drop by drop, and the Petri dish agitated to insure a thorough mixing of the fluids. The whole was allowed to stand for twelve hours at laboratory temperature, after which the solution was diluted to about 40 cc. and the undissolved material collected by centrifuging. The sediment was washed once or twice in the centrifuging tubes with distilled water and again sedimented by centrifuging, then (to remove the water) washed in the same way twice with acetone and twice with ether (dried over calcium chloride). The sediment was then spread out with a glass rod on the inner wall of the centrifuge tube and the remaining ether evaporated by short heating on the waterbath."

The polysaccharide fraction of the peat was then subjected to hydrolysis. "The material was thoroughly mixed with sulphuric acid (1 cc. or less of an 80 per cent solution) and was allowed to stand for three hours, after which water was added and the solid residue collected by centrifuging and thoroughly washed with distilled water as described above. The water was then poured off and lactophenol (according to Amann, phenol crystals (20 g.), lactic acid (20 g.), glycerine (40 g.), aqua destillata (20 g.)) added up to a certain volume, *e. g.*, 2 cc. Staining was effected by adding a small drop of very dilute methylene blue. The whole was mixed carefully and a certain quantity, *e. g.*, 0.1 cc., transferred to a counting chamber."

The purpose of the present paper is to present a simple method which will not involve expensive apparatus and which will separate the pollen grains from the opaque colloidal mass surrounding them without any distortion or breaking.

TECHNIQUE

From the center of the core of the peat borings a lump about the size of a pea was removed with forceps and placed into a 10 cc. vial about one-third full of 95 per cent alcohol. The mixture was vigorously stirred with a small camel's-hair brush, care being taken not to press the peat against the glass. Mixtures stirred with a needle or a glass rod showed a high percentage of crushed pollen grains, especially broken wings of coniferous pollen, but these were infrequent when the brush was used. A tiny drop of dilute aqueous methylene blue was added for staining. This stains especially well the spores and pollen grains. The mixture was stirred until the material had become greatly concentrated and most of the alcohol had evaporated. Evaporation can be hastened by holding the vial near an electric light or in a water bath. If the material was to be held for later use, the vial was tightly stoppered. If the peat is allowed to dry, it will adhere tightly to the sides of the vial. The larger floccules in which the pollen grains are embedded were now broken apart.

After the peat had been well separated by vigorous stirring, some of the concentrated sediment was drawn out of the vial with a pipette and placed in the center of a 22 mm. cover glass. To the sediment on the cover glass a drop of 95 per cent alcohol was added. Then the mixture was stirred with the tip of the brush until observation under the microscope showed the pollen grains and the other particles in the smallest floccules pulled apart by the force of the alcoholic evaporation. If some floccules were undissolved, more alcohol was added and the stirring repeated. Any large pieces of stem or grit were removed with the forceps or tip of the brush. The amount of concentrate taken should not be too small to insure a large number of pollen grains per unit area. If the pollen grains are infrequent, a larger amount of peat can be put into the vial in the same amount of alcohol to increase the number of grains per unit area.

After most of the alcohol had evaporated, but while the material was still moist, a small drop of pure glycerine was added and mixed with the sediment on the cover glass. Finally the cover glass was inverted on a slide to which enough glycerine had been added to mount the material.

Care must be taken not to spread the mixture on the cover glass to the edge when stirring, and not to add too much glycerine or the pollen grains will ooze out at the edges.

DISCUSSION

All workers in the field of fossil pollen recognize the fact that it is impossible to obtain a pure mixture of pollen grains entirely separate from the other materials with which they occur. But it is necessary and possible to loosen the pollen grains from the colloidal masses in which they lie embedded and to prepare a fairly homogeneous mixture in which all particles are separate and distinct when viewed under the microscope. To accomplish this without introducing sources of error means that pollen grains must not be broken, distorted or strained out. Every time some of the coarser débris is removed by straining through cotton or wire gauze, many of the pollen grains are also removed, especially if straining occurs before deflocculation. After deflocculation, the more nearly spherical and smoother grains would tend to pass through easier than rough and knobby grains.

To identify the pollen of Abies, Picea and Pinus, the size of the wings is a most important factor, hence any method which causes many wings to be broken will introduce error on pollen representation. Observations showed that the wings may be broken off even when the peat mixture was stirred vigorously with a needle or a glass rod. Broken or fragmentary grains make identification uncertain, thus giving the advantage to the other pollen grains when the counts are made.

The author has not had the opportunity to work with the new method described by Erdtman (4), but since even stirring with a glass rod resulted in many broken and distorted coniferous pollen, it appears that such a vigorous procedure of separation would of necessity introduce a serious error in a pollen spectrum.

A diversity of opinion exists as to the number of pollen grains to count for trustworthy results. Sears (6) says it is not sound practice to base estimates on counts of less than 100 grains. Bowman (2) counted from 1,000 to 1,800. Lewis, Cocke and Patrick (3) claim that when the number of species is large, a count of less than 1,000 grains is not recommended for accuracy, but that in most cases a count of 500 is reliable. Potzger (5) found no appreciable differences in percentages between counts of 100 and 200 grains.

Barkley (1) made a mathematical study of the problem and says: "The conclusion is that little or no validity accrues from counting above 200 grains per slide. An increased validity would undoubtedly be obtained by averaging counts or samples from correlated layers in two or more adjacent borings. No significant advantage was observed in counting under low power rather than under high power or vice versa."

The method presented in this paper was first tried on peat collected by Potzger from Bryant's Bog, which is located near the southwest corner of Douglas lake in Cheboygan county, Michigan. The peat is moist, loosely packed and comparatively free from soil particles. The samples for experimentation were taken from 2, 3.5, 9 and 10 foot levels. The 9 and 10 foot levels show especially abundant coniferous pollen, and the 2 and 3.5 foot levels abundant Tilia pollen. Thus the effect of the method of separation on two very different types of pollen could be studied. Complete deflocculation was obtained without distortion or injury to the pollen grains and counts of 200 could easily be made from all slides prepared.

Further experiments were tried on peat collected by Russell Artist from Cedar Creek Bog, Anoka county, Minnesota, an alkaline lake type, at depths of 4.5 and 10.5 feet, and from Volo Bog, Volo, Illinois, at depths of 6.4 and 8.6 meters. The peat from Minnesota contained a large amount of gritty material and was mixed with a marly clay, but deflocculation was effected in every case

The successful deflocculation of various types of peat, especially those mixed with an adhesive marly clay, leads the author to believe that the method will work well with all types of peat. When peat shows a small representation of pollen grains, deflocculation can well be followed by centrifuging. However, each type of peat presents its own problems and further experimentation will be necessary to determine whether or not the method will need modifications.

The author wishes to thank Dr. J. E. Potzger for suggesting this problem and for many helpful hints given while the work was in progress.

LITERATURE CITED

1. Barkley, Fred A. The statistical theory of pollen analysis. Ecology 14:283-289. 1934.
2. Bowman, Paul W. Study of a peat bog near the Matamek river, Quebec, Canada, by the method of pollen analysis. Ecology 12:694-708. 1931.
3. Cocke, E. C., I. F. Lewis and R. Patrick. A further study of Dismal Swamp peat. Amer. Jour. Bot. 21:374-395. 1934.
4. Erdtman, G., and H. Erdtman. The improvement of pollen-analysis technique. Sv. Bot. Tids. 27(3):347-357. 1933.
5. Potzger, J. E. Succession of forests as indicated by fossil pollen from a northern Michigan bog. Science 75:366. 1932.
6. Sears, Paul B. Common fossil pollen of the Erie basin. Bot. Gaz. 89:95-106. 1930.

BOOK REVIEWS

THE PRAIRIE

Weaver and Fitzpatrick[1] have continued the series of studies on the Prairie. The present contribution deals with the biotic content and relations. The study is dynamic throughout. The reader not only feels the immensity, but also the vital struggles of the plants both with each other and with the climatic and other environmental factors. Distribution studies, root competition, stem coverage, soil, evaporation, moisture, climatic conditions, ecological associations, growth habits of individual species are studied in great detail and give the reader such a dynamic viewpoint as to make him feel the life throbs of this vast American area. Of the plants listed as characteristic of the prairie, one is struck with the high percentage which occurs to greater or less extent outside the natural prairie area, indicating at once the adaptation possible in some species and the degree to which prairie conditions are found outside the usually recognized area. This study has rendered a real scientific service to students of ecology and plant geography.—RAY C. FRIESNER.

ORNAMENTAL PLANTS

Dr. Stout[2] in his "Daylilies" has performed a most useful service to both the technical botanist and the ornamental gardener. For the technical botanist there is given a detailed description with an analytical key and an account of the distribution of the species within the genus. For the gardener and horticulturist there are given, in addition to the above, the horticultural clons, together with their evaluation, the uses, culture, care and propagation of daylilies. Thirty-six excellent plates are included.

HIGH SCHOOL METHODS

It would seem that Dr. Hunter's latest book[3], "Science Teaching," is the final result of his long series of others. He has attempted to bring together and properly evaluate the newer methods and results of research in science teaching in secondary schools. To the teacher earnestly attempting to apply the more recent findings in education to teaching methods in science, this book presents a valuable aid.

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[1] WEAVER, J. E., and F. J. FITZPATRICK. The Prairie. Ecol. Monog. 4:109-295. 1934.

[2] STOUT, A. G. Daylilies: The wild species and garden clons, both old and new, of the genus Hemerocallis. Pp. x-119. New York: The Macmillan Company. 1934.

[3] HUNTER, GEORGE W. Science teaching at junior and senior high school levels. Pp. VIII-552. New York: American Book Co. 1934.

In Hunter and Knapp's[4] Mastery Tests in General Science and Hunter and Kitch's[5] Mastery Tests in Biology, we have four series of valuable aids to both learning and teaching. Their primary aim is to stimulate careful reading and accurate thinking. In our opinion these tests meet the most fundamental objection we have had to published tests generally; *i. e.,* they measure more than mere factual content; they not only stimulate the pupil to straight thinking, but also measure the quality of thought. Two sets, *viz.,* Set x and Set y, are offered in each of the above fields. They are recommended to every teacher of these subjects in the secondary schools.—RAY C. FRIESNER.

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[4] HUNTER, GEORGE W., and ROY A. KNAPP. Mastery tests in general science. Sets x and y. New York: American Book Co. 1934.

[5] HUNTER, GEORGE W., and LORAN W. KITCH. Mastery tests in biology. Sets x and y. New York: American Book Co. 1934.